VARIABILITY IN THE RATES OF GROWTH AND DEVELOPMENT IN MARINE FISHES AND THEIR EFFECT ON THE TIMING OF EARLY LIFE HISTORY TRANSITIONS

HUGUES PASCAL BENOIT

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VARIABILITY IN THE RATES OF GROWTH AND DEVELOPMENT IN MARINE FISHES AND THEIR EFFECT ON THE TIMING OF EARLY LIFE HISTORY TRANSITIONS

by

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Abstract

There is considerable variability in the timing of early life history transitions within and among species of marine fishes. Variability in the ages and sizes at which fish undergo metamorphosis, from larvae to juveniles, may be particularly important in determining survival because metamorphosis represents the culmination of a period of high mortality and corresponds to a stage by which recruitment levels begin to be established. Using a combination of empirical multi-species literature reviews, experiments, and simple analytical modelling, I show that variability in size and age at metamorphosis results from the integration of the variability occurring throughout early development.

Analysis of several published studies indicates that average metamorphic length is relatively constant within species and mean metamorphic age is the time that it takes to grow to that length. Results from the empirical literature review and from experiments with yellowtail flounder (*Pleuronectes ferrugineus*) demonstrate that differences in the growth trajectories of individual larvae result in considerable variability in metamorphic age, and to a lesser extent length, within populations. Furthermore results from a growth reconstruction study using otolith growth diameters suggest that the metamorphic age of individuals may be predicted by the size that larvae have achieved two weeks after hatch. Sources of such variance in "initial" body length were considered in a second experiment, which demonstrated that the hatching length of yellowtail flounder larvae is determined by interactions between rearing temperatures, maternally derived differences in egg diameter and individual differences

in development time. These interacting variables result in considerable, environment-dependent scope for variability in initial larval lengths.

I conclude by making empirical (multi-species) comparisons of individual-level variability in stage duration and length of larvae at hatching and metamorphosis. In doing so I argue that differences among individuals are generated in a fairly consistent manner for developing embryos and larvae. As a consequence, individual developmental trajectories may begin to diverge soon after fertilization, resulting in considerable variability in the timing of metamorphosis. These results are corroborated by a simple analytical model for autocorrelated individual growth. Overall, the results presented in this thesis suggest that small differences in body size or development rate among individuals occurring early during ontogeny can affect events that occur months later, and may determine eventual chances for survival.

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List of Abbreviations and Symbols

AM: Mean age at metamorphosis (days).

ASE: Asymptotic standard error, used for nonlinear line-fitting algorithms

CV: Coefficient of variation.

DT: Development time. Time in hours from egg fertilization to hatching.

HL: Hatching length (mm).

LM: Mean length at metamorphosis (mm).

MG: Mean growth rate ($mm \cdot day^{-1}$).

MS: Mean Squared Deviations (i.e., variance).

SD: Standard deviation (note that SD_{AM} and SD_{LM} are the standard deviations for age and length at metamorphosis respectively).

SE: Standard error.

SL: Standard length, from the tip of the snout to the posterior most tip of the caudal peduncle.

T: Temperature (°C).

TL: Total length, from the tip of the snout to the tip of the caudal fin.

All other symbols, such as those associated with equations, are explained in the text as they occur.

Chapter 1

General Introduction

Rationale

The early life history of marine fishes represents a period during which rates of mortality are high and variable, resulting in a decrease over several orders of magnitude in the number of individuals (Dahlberg 1979; Sissenwine 1984; Pepin 1991). Survival through early life is extremely sensitive to rates of growth and mortality (Houde 1987; Beyer 1989), and as a result this period has been suggested to be important in influencing variability in adult fish densities (Hjort 1914). More recent studies have shown that the majority of marine fish mortality is concentrated during the egg and larval stages, resulting in survivor numbers in the juvenile stage that begin to reflect eventual survival to recruitment or adulthood (Bradford 1992; Bradford and Cabana 1997). It is this result that prompted the work presented in this thesis. The thousands of fish in a cohort that survive beyond metamorphosis represent a mere subset of the millions that were produced. By studying those individuals lucky or fit enough to survive early life, we may be able to understand which properties, if any, conferred an advantage to them (e.g. Crowder et al. 1992).

A study of marine fish early life history variability is particularly appropriate because the same factors that integrate over time to determine the timing of early life history transitions also appear to directly govern rates of production and survival. Examples of such variables are temperature (and its effect on growth rate) and body size (Miller et al. 1988; Houde 1989a; Pepin 1991; Houde and Zastrow 1993).

However these analyses have focused mainly on species-level responses and may not apply to different stocks of a species or to individual fish (e.g., Chambers et al. 1988; Pepin and Miller 1993). As Pepin (1991) concludes, effort needs to be directed towards characterizing the vital rates (metabolic, growth, mortality) at the level of the individual, where the potential for selection resides (Sharp 1987). In the chapters that follow I will show how small differences in body size and growth rate can result in large differences in the life histories of different species, different populations of species and individuals within populations.

Thesis Outline

The organization of this thesis reverses the normal progression of ontogeny in order to follow logically from the questions raised in the previous chapters. I begin by discussing metamorphosis and then evaluate the determinants of hatching (success, body length and development time) variability. I conclude with a comparison of these two events, and a broader discussion of how individual-level variability is generated throughout ontogeny, from egg production through fertilization, and to metamorphosis.

Chapter 2 reviews the importance of the timing of metamorphosis as a possible determinant of survival variability in a variety of species, and considers the current theories on the determinants of metamorphosis timing. That chapter also serves as a broad introduction to the causes and consequence of early life history variability, and sets the stage for the chapters that follow. As such, I will avoid redundancy by using this short introductory chapter to present the logical flow of the chapters that follow.

From Species to Individuals: Understanding Early Life History Variability

The vast majority of the information regarding the timing of metamorphosis in marine fishes exists for the species level (see Chambers and Leggett 1992). This information is typically contained in multi-species volumes and most often consists of a single metamorphic length for each species (e.g., Moser et al. 1984; Fahay 1983), which is often based on few measured specimens. This sort of information is useful in making phylogenetic comparisons of metamorphic size (e.g., Chambers and Leggett 1992), but it ignores the substantial variability that may occur among and within populations, resulting from temporal and spatial environmental variability (e.g., Fonds 1979; Seikai et al. 1986; Minami and Tanaka 1992). Furthermore, the increasing use of otoliths to age newly metamorphosed (or settled) fishes has resulted in a large literature of fish transition ages (e.g., Brothers et al. 1983; Victor 1986b; Wellington and Victor 1989). This information on metamorphic ages and sizes is synthesized in chapter 2, where the relative magnitudes of inter- and intraspecific variability in metamorphic traits are evaluated and compared. Such a meta-analysis is useful in evaluating trends across species that occur on a wider scale (e.g. across a greater diversity of environments, or across a wider range of life histories) than those that are intraspecific (Myers 1997).

Although the literature on marine fishes contains information predominantly on the average metamorphic ages and lengths for populations and species, there are more limited data on the response of individuals within populations. These data are typically presented as a measure of dispersion surrounding average responses, or as a within-

population correlation between age and length at metamorphosis. The change in dispersion of metamorphic traits as the mean response increases is considered in Chapter 2, because other authors have suggested that means and dispersions should be positively related (Houde 1989a; Chamber 1993). I will argue in chapter 2 that the shape of these relationships provides information on the mechanism that generates individual variability in metamorphic age and size, namely individual differences in growth and development rates. This factor has been poorly understood because of the difficulty in rearing individual larvae in isolation (e.g. Bertram et al. 1997). Consequently, with the experiments that I present in the following chapters, I aim to provide better understanding of individual differences in growth and development during early life.

To elucidate the factors that influence the timing of individual life history transitions, yellowtail flounder (*Pleuronectes ferrugineus*) were reared to metamorphosis in three different temperature treatments (which served to manipulate the growth rates of the larvae). The goals of the experiments presented in Chapter 3 were to describe the probability distributions of ages and lengths at metamorphosis under different growing conditions, and consider how the distributions change with average growth rates. I was also interested in how individual differences in growth trajectories affected individual metamorphic traits. This last question was addressed using the relationship between otolith diameter and body length to recreate individual growth histories, that could subsequently be correlated with the eventual length and age of larvae at metamorphosis. The results presented in Chapter 3 suggest that individual

differences in metamorphic timing may be influenced by differences in length and growth rate occurring early in the larval period (e.g., Crowder et al. 1992).

The importance of early events influencing the body size and growth rate of young larvae motivated the second set of experiments that considered the individual-level variability in development time and hatching length of yellowtail flounder eggs. Chapter 4 deals with the interaction between the environment (rearing temperatures), and maternally-derived differences in egg size in determining individual variability in hatching length. This experiment was conducted because hatching size variability within cohorts is poorly understood (but see Chambers et al. 1989), despite the considerable information that exists at the species and population levels (for a review see Chambers 1997). It is believed that maternal effects on egg size and yolk volume contribute substantially to this individual level variability (Chambers and Leggett 1996). However to date, there were no studies in marine fishes that have considered how the importance of these maternal effects varies with differences in the egg-rearing environment. Filling this gap fits in well with one of the major themes of this thesis, namely the partitioning of individual variability in to that due to the environment and that due to individual differences.

In the final chapter, I present empirical and analytical models that support the observations of the previous chapters, and that allow me to infer the mechanisms that result in individual differences in transition timing and probabilities for survival. I draw upon results from a literature review on individual variability in the timing of hatching in marine fishes, and compare the rate at which individual variability in stage

durations and transition lengths is generated for hatch and metamorphosis. From this I make inferences on the manner in which individual development trajectories diverge through ontogeny, beginning after fertilization. I then explore the causes of these divergences using a simple analytical model for autocorrelated growth. The results from this model and from the empirical relationships for eggs and larvae are then used to determine the extent to which small initial differences in body size or developmental stage can influence individual timing of metamorphosis. Using a simple model for the mortality of marine fish early life stages, I will argue that these small initial differences can also determine individual chances for survival through early life.

Overall I will show that a combination of environmental effects and properties of individual fishes result in considerable scope for recruitment variability given simple assumptions regarding mortality. However, I will also demonstrate that if individuals vary in predictable ways when considered over all of early ontogeny (i.e., individual level variability is generated in a continuous manner), *individual* differences in the probability of survival beyond metamorphosis may also be predictable.

Chapter 2

Patterns of Metamorphic Age and Length in Marine Fishes, From Individuals to Families

Abstract

This chapter presents a summary of age and length at metamorphosis, and associated variability, for marine fishes. Data from the literature were partitioned into taxonomic, population, and individual levels of resolution in order to examine the factors that affect the timing (age and length) of metamorphosis. Temperature appears to be a dominant influence on the timing of metamorphosis in marine fishes. This is likely due to the strong relationship between temperature and growth rate ($mm \cdot day^{-1}$) for fish larvae, and fish in general. When considered interspecifically, length of larvae at metamorphosis was poorly correlated with their size at hatching, but it was significantly and positively related to temperature. This pattern was inconsistent for population level comparisons. Age at metamorphosis showed a strong exponential decrease with increasing temperature in inter- and intraspecific (population level) comparisons, but age did not covary with length for either level of resolution. These results suggest that within species, age at metamorphosis largely is a reflection of the time that it takes to grow to a given metamorphic length. Within populations, the correlation between age and length at metamorphosis among individuals increases exponentially with increasing growth rate, and can be explained by the population variance in metamorphic age and length. A strong exponential relationship between

mean age and length at metamorphosis and their associated variability (SD) exists, with a slope greater than unity in both cases (i.e., variability increases relative to the mean). The shape of these relationships allow us to make inferences to the manner in which individual level variability in metamorphic traits is generated throughout ontogeny. These results are considered in light of recruitment variability in marine fishes.

Introduction

There is ample evidence that simple stock-recruitment relationships are not sufficient to explain and predict the dynamics and variability of fish populations (summarized in Rijnsdorp 1994, but see Fogarty 1993; Iles 1994). Furthermore, general biological characteristics of adult fishes, such as fecundity, correlate poorly with recruitment and its associated variability (Rothschild and Dinardo 1987; Bradford 1992; Mertz and Myers 1996). Although large scale climatically driven environmental factors, such as currents and temperature, can significantly impact pre-recruitment survival (Norcross and Shaw 1984; Koslow 1984; Sinclair 1988; Myers and Pepin 1994), there is growing emphasis directed at the level of the individual, where the potential for selective mortality occurs (Chambers and Leggett 1987, 1992; Rice et al. 1993). In particular attention is being turned away from trying to explain what causes >99% of a cohort to die within a short period of time, to focusing on which factors allow the <1% of the population to survive. Knowledge of the characteristics of survivors through different developmental stages may help explain the dynamics witnessed at the stock level (Sharp 1987), as the mean, dispersion and distribution of

those traits may be important determinants of survival patterns (Pepin 1989; Rice et al. 1993).

Mortality in most marine fishes is concentrated in the early life, during which the rate is large, variable, and typically density-independent (Dahlberg 1979; Sissenwine 1984; Bradford 1992). Furthermore, densities of fish at the end of the larval stage begin to correlate with recruit densities, indicating that relative cohort size is generally established around metamorphosis, with some density-dependent fine-tuning thereafter (Zijlstra and Witte 1985; Victor 1986c; Veer et al. 1991; Beverton and Iles 1992; Bradford 1992; Rijnsdorp et al. 1992; Myers and Cadigan 1993a,b; Leggett and DeBlois 1994; Rose et al. 1996; but see Peterman et al. 1988). Although the high fecundity of most marine fishes suggests a stochastic, non-selective source of mortality during the egg and larval stages, many processes appear to result in selective mortality (Anderson 1988; Miller et al. 1988; Houde 1989b; Pepin 1991; Paradis et al. 1996; Miller 1997). Consequently, it may be more appropriate to question when and how selective mortality changes over the early life history. It has also been argued that the effects of time on cumulative mortality (i.e., longer exposure to mortality factors), may be equally or more important in affecting recruitment variability than instantaneous individual traits, such as size-at-age (Houde 1987; Beyer 1989; Pepin and Myers 1991; Bell et al. 1995). Regardless of the mechanism, differential survival among individuals has the potential to be important given that larvae reared under identical growing conditions exhibit considerable variation in life history parameters (Policansky 1982, 1983; Chambers and Leggett 1987, 1992). Subtle differences in metamorphic life

history traits (e.g., size and age) could have significant impact, because relatively small changes in mortality, growth or stage duration in the larval life history of fishes can potentially create large fluctuations in recruitment (Houde 1987, 1989; Beyer 1989; Pepin and Myers 1991).

The ecologically significant aspect of metamorphosis in many marine larvae is the occurrence of a niche shift, whereby larvae change trophic status and/or habitats (see Houde 1997a). For many species, the larval stage occurs in pelagic, open waters (a three-dimensional habitat), and individuals settle to the demersal zone around metamorphosis. In some species such as flatfish (e.g., sole, plaice, flounder) metamorphosis involves a radical reorganization of morphology, presumably as an adaptation to a two-dimensional benthic existence (see Osse 1990). Policansky (1983) suggests that aspects in each habitat that influence larvae and juveniles differently (food particle sizes, predator types, competitors), would result in body size as the main cue for metamorphosis, and settlement. This forms the basis for niche shift theory (Werner and Gilliam 1984) whereby size-dependent growth and mortality influence timing of metamorphosis (Werner 1986; Houde 1997a).

In contrast, if settlement is seasonally triggered (e.g., lunar cycles), larval age may determine the timing of settlement. Otherwise, if organisms inhabit randomly fluctuating environments where the duration of the fluctuation is less than that of the larval stage, selection may favor plasticity in age and size at metamorphosis (see Thompson 1991 for a review of the adaptiveness of plasticity). For example, if settlement is cued by specific suitable settlement sites, pelagic larvae which are at the

mercy of currents may have variable age and/or size at metamorphosis (Jenkins and May 1994). Despite the lack of a firm understanding of the factors that influence metamorphosis in marine fishes, a general conclusion is that the timing is not a haphazard process, as the existence of a complex life cycle is indicative of selective pressures which change with the size or age of an organism (Werner 1988).

Patterns of Age and Size at Metamorphosis in Non-fish taxa

Population level variability and individual plasticity in age and size at metamorphosis has been extensively studied in anurans, although some work has been done with other amphibians, as well as invertebrates (e.g., Wilbur and Collins 1973; Travis 1984; Alford and Harris 1988; Pfenning et al. 1991; Leips and Travis 1994; Bradshaw and Johnson 1995; Twombly 1996). Several qualitative and quantitative models have been proposed in an attempt to explain the patterns of transition times and sizes. Although most of the models were developed for anuran metamorphosis, their broad applicability to any organism undergoing fairly dramatic morphological changes accompanied by a niche shift, warrants discussion.

Wilbur and Collins (1973) proposed that development or differentiation (the change in form or developmental stage with respect to time) is flexible throughout the larval period and that age and size at metamorphosis are dependent on recent growth history. In the Wilbur-Collins model, larvae metamorphose within bounds of minimum and maximum sizes, and at a point when instantaneous growth rate falls below some critical level, so as not to incur the costs of continued poor growth. If recent growth has

been poor, the larvae will undergo metamorphosis either immediately (if larger than the minimum size) or at the minimum size once achieved. If recent growth has been good, individuals will continue to grow until the maximum size, and consequently only age will vary.

Others have argued that the rate of larval development is inflexible for older larvae, and that age at metamorphosis is set earlier in the larval period (Travis 1984; Hensley 1993; Leips and Travis 1994). As body growth depends on environmental factors such as food availability, variability in size at metamorphosis is mainly influenced by growth once the rate of development is set.

Given that both views of metamorphosis, that of flexible development (Wilbur and Collins 1973) and of ontogenetic loss of flexibility (Travis 1984; Hensley 1993; Leips and Travis 1994), are concerned with the effects of varying larval growth rate (especially rates immediately preceding metamorphosis), tests have consisted of growing larvae at a particular rate, and increasing or decreasing the rate of growth at various intervals during development. The results of such manipulative studies have yielded inconclusive results both within and among studies (Travis 1984; Alford and Harris 1988; Hensley 1993; Leips and Travis 1994; Tejedo and Reques 1994).

A third model of amphibian metamorphosis has treated the process as a niche shift (Werner and Gilliam 1984), and considered it adaptively in the context of pre- and post- metamorphic contributions to an organism's fitness (Werner 1986, 1988; Rowe and Ludwig 1991). The "decision" to undergo metamorphosis represents a balance between maximizing growth and minimizing mortality (two factors that vary with an

organism's size) across the habitats occupied by larvae and juveniles. Furthermore, if fitness is influenced by time (e.g., if important life history events are restricted to particular seasons), optimal sizes for niche shifts may vary with time (Rowe and Ludwig 1991). Models that treat metamorphosis as a niche shift are attractive both because they present a quantitative framework for considering metamorphosis and they take an ultimate (adaptive) view of the process, compared to the models of flexible (Wilbur-Collins) and fixed development (Leips-Travis). Nonetheless, the importance of growth rate is a common characteristic of all the models of metamorphosis timing.

Patterns of Age and Size at Metamorphosis in Fishes

Manipulative experiments dealing with the timing of metamorphosis, such as those cited in the previous section, have not been performed for marine fishes. Studies of fish metamorphosis, both in the lab and the field, are largely observational. Nonetheless, by comparing patterns for metamorphic traits (e.g., effect of growth rate on age and size at metamorphosis) among taxa, generalities may become apparent and it may be possible to postulate mechanisms that generate variability in life histories. Consequently, interspecific comparisons are useful in forming null hypotheses and in designing experiments for intraspecific studies (Pepin and Miller 1993). Furthermore, although these comparisons cannot be used to test the predictions of the models of metamorphosis presented previously, they allow us to consider the scope for variability in the timing of metamorphosis. This is the goal of the present review.

Knowledge of the patterns of covariation between age and size at metamorphosis in fishes is limited, as people generally assume a fixed metamorphic size within a species, with metamorphic age as the time it takes to grow to that size. Although there is a vast record of metamorphic size of fishes, and to a lesser extent ages (see Appendix 1), few studies have comprehensively synthesized this information (e.g., Houde 1989a; Chambers and Leggett 1992; Houde and Zastrow 1993). Assuming that metamorphic weight was constant within species, Houde (1989a) and Houde and Zastrow (1993) calculated metamorphic age of several species of marine fish as the weight gain from hatching to metamorphosis divided by mean growth rate. From an observed positive relationship between growth rate and temperature, it followed that metamorphic ages (and associate variability) and temperature varied inversely. Chambers and Leggett (1992) focused on metamorphosis in flatfishes (Pleuronectiformes), by summarizing information at different levels of organization: individuals, populations and species. At the population level, they confirmed that metamorphic ages increase with decreasing temperature. At the individual level, the authors found that size at metamorphosis may be influenced by parentage (mainly maternal), although the interaction with temperature was not investigated.

The reviews of Houde (1989a), Chambers and Leggett (1992), and Houde and Zastrow (1993) advanced significantly our understanding of metamorphosis in fishes, but also left many unanswered questions. One of the observations of Houde (1989a) was that as metamorphic age increased, so did its associated variability. Unfortunately, because variability in age was calculated from the range of observed growth rates for a

given species, rather than estimated directly, it is not possible to establish the form of the relationship between average metamorphic age and its associated variability. Furthermore, no distinction can be made between the range of mean metamorphic ages among populations of a species, and the variability among individuals within a population. A consideration of the relationship between the mean and variability in larval stage duration is important because the former affects the temporal exposure to high and variable mortality rates, and the latter represents the extent to which individuals differ in this exposure. As the two reviews highlight the importance of size in triggering metamorphosis, other unanswered questions include what aspects influence size at metamorphosis and to what extent metamorphic size is plastic within species and within populations. Furthermore, Chambers and Leggett (1992) had too few populations to determine the patterns of correlations between metamorphic age and size at the level of the individual.

In this chapter I extend previous studies by including new data which has appeared since those reviews, as well as including data from many taxa which allows me to elucidate and infer the causes of age/size variation at the level of the individual. Data at all levels of resolution are included in this review in order to make empirical predictions for taxa, populations and individuals. My objective is to examine how life history, environmental conditions and phenotypic plasticity interact, and to propose how this interaction may influence differential survival among individuals.

Data Sources and Analyses

The scientific literature was surveyed for information pertaining to the life history features associated with metamorphosis in marine fishes. The parameters of interest included age and length at metamorphosis, the variability surrounding these parameters, as well as factors which influence metamorphic age and length (including growth rate and temperature). As the goal of this review was to establish the scope and patterns of variability in metamorphic traits, I only include species for which information on two or more of the parameters listed above was available, or for which data on more than one population exist. Consequently, this excludes information on metamorphosis obtained from general multi-species volumes (e.g., Fahay 1983; Moser 1984), which generally consists of a single, average metamorphic length reported for each species. Weight at metamorphosis, which is an important indication of condition and body shape in fishes (when considered jointly with body length), was also excluded from the current review because data on this variable with accompanying (directly measured) stage durations are scarce. The species used in this review, the level(s) of interpretation (resolution) possible for each taxa given, as well as all data sources are given in Appendix 1. Levels of resolution include family, species, population and individual levels (see below).

Metamorphosis is generally defined as the attainment of adult characteristics following a change in non-reproductive structures at the end of larval life (Yousson 1988), although a precise definition of what constitutes the completion of metamorphosis varies among species. I further expanded this definition to include

settlement of larvae as is typical of reef fishes, because the timing of these niche shifts associated with metamorphosis has important implications for the fitness of fish (Werner 1988; Houde 1997a). Consequently, although larvae may settle slightly before or after undergoing "morphological" metamorphosis, I include them because the habitat transition is abrupt, often occurring overnight (Sale 1991), suggesting that the timing of settlement may be important for survival.

Many species that were included in Houde's (1989a) review have been excluded for the purpose of this chapter. Taxa such as Clupeiformes (Clupeidae and Engraulidae- herrings, sardines, shads, anchovies), Gadiformes (cods, hakes), Perciformes (Serranidae, Percidae- porgies, rockfish, sea bass) and Scombroidei (mackerels, tunas), have very progressive larval developments, with little or no abrupt, rapid change in external morphology at metamorphosis. Consequently, metamorphosis is typically subjectively considered as the attainment of a given body size. Furthermore, unlike the reef fish mentioned in the previous paragraph, niche shifts in these taxa are progressive, and it is difficult to precisely determine when an individual has truly adopted a benthic existence (e.g., Lomond et al. 1998). Both of these factors preclude any analysis of variability surrounding metamorphic size, and they limit the precision with which metamorphic or settlement age can be determined. Exceptions were made for species reared in the laboratory for which non-subjective criteria for scoring metamorphosis were used, allowing for quantification of the variability mentioned above.

For the life history parameters listed above, I was interested particularly in compiling data for different levels of organization, namely data for species, populations within species, and for individuals within populations. Taxonomic family level comparisons were also made for the traits that pertain to individual variability (see *Analysis* section). For the purpose of this review I consider different populations as any assemblage of individuals of a species that were reared or developed together as a group, and consequently experienced similar environmental conditions throughout development.

The reasons for taking a hierarchical approach to my synthesis are twofold: firstly, the selective pressures may differ across levels, and secondly, inferences made at one level may not hold at another (Chambers et al. 1988, 1989; Chambers and Leggett 1992; Pepin and Miller 1993). Data analyzed at the resolution of species allow inferences regarding life history and phylogeny, population level resolution allows for inferences on phenotypic plasticity (i.e., interaction of genotype and environment), and individual level resolution explores patterns of trait covariation as well as familial and environmental contributions to variation (Chambers and Leggett 1992; Chambers 1993). Nonetheless, patterns observed at coarser levels of resolution (e.g., species level), are useful in creating hypotheses for studies at finer resolutions (Pepin and Miller 1993).

Data for populations within species typically came from different studies, and therefore from different environments (Appendix 1). Although this provided the opportunity to examine patterns for different growth regimes, it created the potential for

errors due to varying protocols between studies. This was a problem at all levels of organization, particularly because age at metamorphosis was determined either by the time from hatch to metamorphosis in rearing experiments, or was back calculated from otolith increments in studies of wild populations. I was unable to account or correct for errors in age back-calculation, however, an attempt was made to eliminate studies in which the results of otolith counts were dubious. Studies which calculated metamorphic age as the date of disappearance of larvae from the plankton (i.e., settlement) minus the date of spawning were not included as estimates based on this method are very inaccurate.

Another potential source of error is that I could not always correct for whether studies presented larval length as standard length (SL), the tip of the snout to the end of the notochord, or total length (TL), which includes the caudal fin, because correction factors were not available for all taxa. I feel that this source of error would be small though relative to interspecific variability, as the correction has only a relatively small effect on estimated length (<10%). I was also unable to account for whether authors presented body lengths as measured fresh or measured after preservation. Few studies (<5%) did not account for effects of preservation on lengths of fish. As before, I feel that the error that this would add to my review is minimal, as effects of preservation and handling on lengths are small relative to differences in length among species (see Pepin et al. 1998). Lastly, some of the error in my review may stem from cases in which mean or variance estimates of metamorphic age or length had to be extracted from

graphs, resulting in a lack of accuracy in the true estimate (these cases are noted in Appendix 1).

Growth rate is an important factors influencing life history parameters (Houde 1989a). For the purpose of this study, growth rate growth ($mm \cdot d^{-1}$) was calculated as: $(L_{metamorphosis} - L_{hatch}) \cdot (\text{age at metamorphosis})^{-1}$, where L is the length of the fish in millimeters, and age was measured in days (from hatch or first feeding to metamorphosis). Only rarely was length at hatch provided for a particular species in a given study, and often a species-wide average was used for all populations in a species. If length at hatch was not given in the study at hand, it was extracted from other studies or from volumes containing information on many taxa (Fahay 1983; Moser et al. 1984; Thresher 1984). For some reef fish species, length at hatch was not available, and a family wide average hatch length was used as a best approximation. Although these factors make estimates of hatch length imprecise, its effect on estimates of growth was judged to be minimal because length at hatch was generally much smaller than length at metamorphosis.

A problem with using growth rate for comparisons with metamorphic age and length is that the manner in which growth is calculated makes it dependent on age and length. This lack of independence precludes any hypothesis testing or estimates of correlation (Atchley et al. 1976), although estimates of slope and intercept are valid and can be compared among taxa (D. Schneider, Memorial University of Newfoundland, *personal communication*). Thus, I will show that mean temperature is highly correlated with average growth rate; it can therefore be used to represent an independent estimate

of potential growth rate. Based on this I present the results of analyses using temperature (as a proxy for growth) in both tabular and graphical form, but analyses considering growth rate are presented in tables only, to conserve space.

Analysis

Correlation analyses were performed using both parametric (Pearson's product-moment) and nonparametric (Kendall's tau) techniques. The nonparametric method assumes a monotonic relation between variables, a weaker assumption than linearity. A comparison of parametric (r) and nonparametric (τ) correlation coefficients provides an assessment of the potential influence of outliers on the strength of the association. Prior to the calculation of the measures of correlation, variables were $\log_{10}$-transformed where appropriate in order to achieve linearity among the variables.

As comparisons among species often included species with information on more than one population, and because these different populations often experienced different growth regimes, I deemed it inappropriate to take an average of the life history variables for each species. Instead, all the populations of a species were included in the analyses, but each population was weighted by the inverse of the number of populations in that species. Weighting was only performed for the parametric correlations, as weighting of nonparametric analyses is inappropriate.

Chambers and Leggett (1992) point out that genetic history (order and family level patterns) can weaken intraspecific correlations. Indeed Houde and Zastrow (1993) found some taxonomic differences in temperature-adjusted growth rates and stage durations, as well as energetics properties of larvae. However the authors conclude that

temperature is a predominant factor affecting these rates and processes, and they are unable to provide explanations for many of the observed phylogenetic differences. In a review such as ours, data are only selectively available for certain species or genera in a family, making it difficult to make unbiased conclusions regarding differences among taxa. Furthermore in comparisons among families there are often a few "outlying" species that are particularly large or fast growing and which disproportionately affect trends in the data. Lastly, the goal of this review is to present patterns and scope for variability in metamorphic traits, rather than making precise (yet likely biased) conclusions about phylogeny. As a consequence I have opted to forgo including phylogeny in my analyses of mean metamorphic traits (age and length), particularly because analyses of this type are presented to an extent elsewhere (Chambers and Leggett 1992; Houde and Zastrow 1993). Family level patterns can, however, be extracted from the figures. In contrast, analyses which consider individual level variability do include phylogeny and a rough categorization of habitat as such analyses are not available elsewhere, and because my review focuses largely on this level of resolution.

I chose the standard deviation (SD) as an absolute measure of variability in the life history variables (age and length) over the coefficient of variation ($100 \cdot SD \cdot mean^{-1}$), a measure of relative variability, for three reasons. First, when calculating the coefficient of variation, both the mean and standard deviation of the sample will have errors associated with them, and their ratio may compound these errors. Secondly, comparisons of mean and associated variability for metamorphic ages and sizes using

coefficients of variation face the same independence problems mentioned previously (Atchley et al. 1976). Lastly, if selective mortality occurs for larval fish, I believe that it will act on the absolute dispersion, and not the relative variability.

Results

I begin this section by establishing the relationship between growth rate and temperature. Following this, taxonomic and among-population variability in each metamorphic life history parameter is investigated separately. This is followed by a presentation of individual level covariability and variability in metamorphic age and length.

Relationship between temperature and growth rate

Mean growth rate increased exponentially with increasing temperature when compared among species ($r=0.82$, $\tau=0.61$, $P<0.0001$) (Table 2.1, Figure 2.1). As wild caught fish ($n=8$) could have experienced more variable temperatures than reared fish ($n=54$), separate growth-temperature analyses were performed. The two groups did not differ significantly in terms of slope (2 sample t-test, $t=1.896$, $df=58$, $P>0.05$), although correlation coefficients for wild fish were somewhat stronger, owing to smaller sample size and the use of a single species (wild fish: slope $\pm$ SE = 1.514 ± 0.147, $r=0.97$, $\tau=0.75$; reared fish: slope $\pm$ SE = 1.977 ± 0.195, $r=0.82$, $\tau=0.57$). Comparisons among populations within species show a similar pattern to interspecific comparisons (Figure 2.1).

The data used in these analyses for growth rate were limited to those cases that were also used in the analyses of metamorphic traits. This is the reason that the majority of the data are from laboratory studies, and are largely composed of flatfish species. However the strong positive relationship between larval growth rate and temperature has been demonstrated for many other species (Houde 1989a; Pepin 1991), although small significant differences in temperature-adjusted growth exist for some groups (Houde and Zastrow 1993).

Length at metamorphosis

Grouping all marine species which had an estimate of hatch length, I did not find a significant parametric correlation ($r = -0.1$, $P=0.241$) between length at hatch and length at metamorphosis, but a weak yet significant nonparametric correlation was detected ($\tau=-0.18$, $P=0.004$), (Table 2.1, Figure 2.2). In contrast, Chambers and Leggett (1992) have found a positive association in flatfish, and it may be that taxa-specific correlations do exist (Figure 2.2), although I emphasize that in the larger scheme, hatching and metamorphic lengths are unrelated.

A significant positive correlation was found between metamorphic length and temperature at an interspecific resolution ($r=0.62$, $\tau=0.38$, $P<0.0001$) (Table 2.1, Figure 2.3). A similar pattern occurs when temperature is replaced with growth rate (Table 2.1). This pattern was not reflected among populations however. Four of 8 species (*Upeneus tragula*, *Pleuronectes americanus*, *Paralichthys olivaceus*, and *Ammotretis*

rostratus) showed a pattern of decreased length at metamorphosis with increasing temperature, although the change in length with temperature was only statistically significant ($p<0.05$) for *Paralichthys olivaceus* (see Minami and Tanaka 1992).

Age at metamorphosis

Age at metamorphosis showed a significant negative exponential correlation with mean growth rate, and concordantly with temperature ($r=-0.71$, $\tau=-0.43$, $P<0.0001$) (Table 2.1, Figure 2.4). The population-level patterns of age and temperature were similar to that among species. This similarity suggests that age at metamorphosis is simply the time it takes larvae to reach their metamorphic length. Consequently, a multiple regression relating log-transformed metamorphic age to both $\log_{10}$(temperature) and $\log_{10}$(length gain from hatch to metamorphosis) was performed to examine the sensitivity of age to the length that must be achieved. The length component was insignificant ($p=0.207$), and explained only 1.2% more of the variance in age, in contrast to a model including only temperature.

Relationship between metamorphic age and length- Species and Populations

There is a weak positive association ($r=0.25$, $\tau=0.03$) between age and length at metamorphosis (Figure 2.5a) which is highly significant for the parametric statistic ($P<0.0001$), but nonsignificant using a nonparametric method (Table 2.1), indicating that the relationship is driven by relatively few points. For those species ($n=6$) which

had enough populations with which to perform an intraspecific regression of length on age, only two showed a significant pattern (Figure 2.5b): *Platichthys stellatus* (slope ± SE = -0.026± 0.009 n=9, r=0.75, P=0.021), and *Sicydium punctatum* (slope ± SE = -0.072± 0.026, n=10, r=0.75, P=0.025). Data for *Sicydium antillarum* were marginally nonsignificant (slope ± SE = -0.063± 0.017, n=4, r=0.93, P=0.07). The lack of a significant relationship between age and length for other species may have been limited by the number and range of observations.

Relationship between metamorphic age and length- Individuals

A very strong exponential relationship (r=0.99, τ=0.77) was found between mean growth (Δlength/age) and the slope of the regression of length on age at metamorphosis, at the resolution of individuals (Table 2.1, Figure 2.6). The relationship was also considered excluding *Upeneus tragula*, and it remained strong and significant. The relationship in Figure 2.6 immediately seems difficult to interpret because both mean growth, and the slope of age on length have traditionally been used as estimates of length gain over time. The distinction to be made here is that the relationship between age and length is not the length of individuals at different instances in time (i.e., longitudinal data), but rather the outcome of different growth processes of different individuals (i.e., a cross-section of the age and length of individuals at the metamorphic climax).

One influential factor for the observed relationship is the relative range of lengths and ages. As average growth rate increases, the standard deviation of length at

metamorphosis increases significantly relative to that of metamorphic age (Table 2.1, Figure 2.6b), consequently, as the range of lengths widens, the slope of the relationship increases. As an extreme example, when the range in metamorphic length becomes very large relative to the range in metamorphic age, the slope will tend to infinity. Another corroborating piece of evidence that the individual level metamorphic length-age relationship is dictated by growth, is the tendency for warmer water fishes to have steeper age-length slopes relative to fishes occurring in more temperate waters (Figure 2.6). Unfortunately, too few studies reported water temperature and metamorphic age-length slopes to quantify the relationship.

Variability in Age and Length at Metamorphosis-Individuals

A strong significant association between log (mean metamorphic age) and the log of its associated variability (SD) was found ($r=0.84$, $\tau=0.70$, $P<0.0001$) (Table 2.1, Figure 2.7). Given that the slope of this relationship is greater than one, SD increased relative to the mean (i.e., the coefficient of variation also increased), indicating that some factors are enhancing variability with respect to that expected due to increasing mean alone. The regressions of SD on metamorphic age for the dominant families included in the data set (Labridae, Pleuronectidae, and Pomacentridae) were compared in an analysis of covariance. The interaction between slope and family was not significant ($F_{2, 153}<0.001$, $P=0.998$), suggesting minimal effects of phylogeny on patterns of individual level metamorphic age variability. Among populations, most species showed a similar pattern for SD on metamorphic age, with *Pleuronectes*

americanus being the only exception (Figure 2.7). An analysis of covariance was also used to compare the slopes for tropical and temperate-boreal species, as some authors have argued that populations of tropical reef fish may have highly variable metamorphic ages, in order for individuals to find suitable settlement sites (Jackson and Strathman 1981; Victor 1986a; Cowen 1991; Jenkins and May 1994). I did not find a significant difference between these two coarse categorization of ecosystem (ANCOVA; $F_{1, 186}$ =0.63, P=0.43).

A strong significant association between mean metamorphic length and its associated variability (SD) was also found (r=0.65, τ=0.53, P<0.0001) (Table 2.1, Figure 2.8), with SD increasing relative to mean length (i.e., slope >1). The regressions of SD on metamorphic length for the two dominant families included in the data set (Pleuronectidae, and Pomacentridae) did not differ significantly in an analysis of covariance ($F_{1, 45}$<0.001, P=0.995). Intraspecifically, the pattern is less clear. Some of the smaller-bodied taxa, such as *Solea solea, Pleuronectes americanus* and *Chromis atripectoralis*, show a tendency towards decreasing SD with increasing body size (over a limited range of lengths). Larger-bodied taxa tend to have increasing SD with size. Unfortunately due to limited sample sizes, I cannot comment on the generality of this pattern. The habitat or ecosystem where larvae reside (tropical and temperate) did not significantly affect the rate at which metamorphic length variability was generated (ANCOVA: $F_{1, 68}$ =2.5, P=0.12).

Patterns of SD for both age and length at metamorphosis were compared to examine if variability in one parameter would affect the variability in the other (Figure

2.9). Correlations between the two variables were poor and insignificant (Table 2.1), a non-surprising result given that mean age and length were poorly correlated. Patterns were not affected by family ($F_{1, 46}$ =0.09, P=0.76) or habitat ($F_{1, 64}$ =0.6, P=0.44).

Discussion

In this study of the patterns of age and length at metamorphosis of marine fishes, separating literature information into the levels of species, populations and individuals has proven to be crucial and informative. Certain variables, such as temperature and its effect on growth rate and metamorphic age, showed consistent patterns across levels of resolution, possibly suggesting that similar mechanisms may be operating. This was not true for metamorphic length.

That mean growth rate was strongly correlated with temperature both among and within species is not unexpected given the physiological basis of temperature effects on growth (Wooton 1990). Similarly, the largely consistent effect of temperature on mean age at metamorphosis, among and within species, points to a "metabolic basis" by which metamorphic age is affected by temperature, likely mediated by growth rate (Houde 1989a; Gadomski and Caddell 1991; Chambers and Leggett 1992; Houde and Zastrow 1993). This may not be ubiquitous, as other authors have argued that temperature and age are important in controlling metamorphosis (Riley 1966), or that length alone cannot be sufficient to trigger metamorphosis due to its change with temperature (Seikai et al. 1986; Minami et al. 1988; Hovenkamp and Witte 1991; Minami and Tanaka 1992).

Intraspecific plasticity in length at metamorphosis in some species may be a consequence of selection on age or may be due to environmental factors such as availability of suitable settlement sites or other settlement cues. As an example, in fishes whose settlement is signaled by lunar cycles (e.g., Thresher 1984; Tanaka et al. 1989b; Sale 1991; Bell et al. 1995), we would not expect relatively fixed sizes at metamorphosis if time becomes an added constraint (but see Sponaugle and Cowen 1994). Consequences of this effect include small variability in metamorphic age, regardless of the magnitude of mean age (as reported by Robertson et al. 1988), and sizes at settlement which result because of the prevailing growth rate from time of hatch to the lunar cycle at which settlement occurs (Bell et al. 1995). Thus, although metamorphic age generally represents the time taken to grow to a relatively fixed metamorphic length, the constraints faced by many larvae restricted to passive drift in currents may force them to be more plastic in their timing of settlement.

Although not examined in this review, it is worth noting that temperature has also been shown to affect the rate and duration of the metamorphic process (i.e., the period when metamorphosis is taking place) (Keefe and Able 1993). As metamorphosis may be a time of decreased feeding (Thorisson 1994) and possibly higher susceptibility to mortality from starvation or predation, temperature may have an important impact on the survival of newly settling fishes.

Despite showing a positive correlation with temperature, mean length at metamorphosis does not appear to have an entirely metabolic basis, as the population-level patterns are inconsistent among species and often inconsistent with the overall

interspecific pattern. This observation, along with the relative constancy of metamorphic length within species (as compared to age), suggests that length at metamorphosis is generally species-specific, and may be an adaptive trait (Chambers et al. 1988; Chambers and Leggett 1992; Osse and Van den Boogaart 1997). Given that many of the factors that affect growth and mortality in marine fishes change in predictable ways relative to body length and temperature (e.g., Miller et al. 1988; Pepin 1991), niche shift theory would predict that body length would serve as a cue for metamorphosis, or a pre-determined end-point of the larval stage (Werner 1986, 1988; Houde 1997a). As an example, Noichi et al. (1997) found that larval Japanese flounder (*Paralichthys olivaceus*) metamorphose at progressively smaller sizes, and lower degrees of ossification, as the growing season progressed. The authors speculate that larvae may be settling early to take advantage of abundant and optimally sized benthic prey.

An interesting result of this review was the pattern of metamorphic age-length correlations within populations (among individuals). The observation that among-populations differences in the regressions of length on age correlated strongly with mean population growth rate, is identical to Newman's (1989, 1994) qualitative result for the spadefoot toad, *Scaphiopus couchii*. In contrast, an opposite pattern has been demonstrated by Tejedo and Reques (1992), working with natterjack toads (*Bufo calamita*) and was tentatively attributed to genetic plasticity. Pfenning et al. (1991) propose that an inverse relationship between age and size would be expected when an

animal is exposed to rapidly diminishing food resources (consistent with the Wilbur-Collins Model).

Newman (1994) explains the pattern of increasing correlation between metamorphic age and size with growth rate by noting that poor correlations occurred where the range in metamorphic sizes was relatively smaller than the range in metamorphic ages. In the *Results* section, I proposed a similar mechanism whereby variability in metamorphic length increased relative to variability in metamorphic age with increasing growth rate. However, in order to explain the observed transition from negative to positive metamorphic length-age correlations we must consider the relationship between metamorphic age and individual growth rates. This consideration is because a positive length-age correlation can have two origins: one where faster growers remain as larvae for longer periods and are both the oldest and largest at metamorphosis, and the other where slower growers delay metamorphosis in order to grow larger than their fast-growing counterparts. In the first case, there is a positive relationship between growth rate and metamorphic age (i.e., faster growers delay metamorphosis the longest), whereas in the latter, this relationship is negative. A negative age-growth relationship may also result in a negative metamorphic age-length correlation if slow growth rates are sufficiently slower than fast ones, and consequently older metamorphs are not able to outgrow younger ones. Therefore the transition from a negative age-length relationship to a positive one should occur when growth rate is negatively related to age at metamorphosis.

The mechanistic explanation for correlations between metamorphic age and length within cohorts highlights another interesting finding of this review, which is the relationships between life history variables and the variability surrounding them (e.g., Victor 1986a; Houde 1989a; Thresher and Brothers 1989; Thresher et al. 1989; Hovenkamp and Witte 1991). The consequences of these patterns can potentially be far reaching given that the mean characteristics of a population alone can influence recruitment variability through their effect on cumulative mortality (Houde 1987; Pepin and Myers 1991; Bell et al. 1995). My findings that variability in metamorphic age increases relative to the mean further compounds the effect of long stage duration (i.e., duration of the exposure to high rates of mortality), by superimposing the variability associated with long duration.

As temperature (and growth rate) declines not only does stage duration increase exponentially, but so does the variability about that duration (see Houde 1989a; Chambers 1993). This may allow us to better understand inter- and intraspecific patterns of recruitment (e.g., latitudinal contrasts, comparisons of early versus late spawning stocks, etc). Data on flounders support this contention whereby increased egg and larval stage durations result in increased recruitment variability (reviewed by Miller et al. 1991). A similar result was found in a latitudinal comparison for American plaice (*Hippoglossoides platessoides*) (Walsh 1994), although Leggett and Frank (1997) show that this latitudinal pattern may not be consistent among species and stocks in a larger study of flatfish recruitment variability. Nonetheless, Leggett and Frank (1997) found that the spatial scale of interannual recruitment variation is of the same order as

variation in wind and sea surface temperature, and the authors speculate that these abiotic factors may be important in determining recruitment variability (a similar result to Myers et al. 1996). I emphasize that what I propose is a link between temperature (or growth) and recruitment variability, not recruitment per se. I acknowledge the various factors that affect marine larval survival, and agree with other authors that simple environmental correlates of year class strength have little predictive power given the error with which variables are measured (Walters and Collie 1988; Bradford 1992; Tyler 1992).

So far, I have discussed the implication of relative variability in age and length at metamorphosis, but I have made no mention of their causes. Some authors working with invertebrates have speculated that the increases in relative variability with increasing metamorphic age may be adaptive, allowing pelagic larvae a greater chance to find a suitable settlement site (e.g., Jackson and Strathman 1981; see Pechenick 1990 for a review of delayed metamorphosis in invertebrates). A similar argument has been applied to fish larvae (Jackson and Strathman 1981; Victor 1986a; Cowen 1991; Jenkins and May 1994). This is based largely on observations that species such as the wrasses *Thalassoma bifasciatum* and *Semicossyphus pulcher*, are capable of delaying settlement by reducing their growth rates, even after they have become competent to settle (Victor 1986a; Cowen 1991). However this phenomenon is limited to a few taxa, and often to a few individuals in a population, leading some authors to conclude that growth rate is likely the most important determinant of metamorphic age (Wellington and Victor 1992; Cowen and Sponaugle 1997). The continuous relationship between

mean metamorphic age and its variability, across several orders of magnitude of both factors, along with the observation that the relationship was generally constant among taxa and populations, point to a non-adaptive nature of variability in metamorphic age.

Stage duration dictates the number of days over which growth occurs, and therefore also dictates the potential for stochasticity in growth. Given that development is a multiplicative process, and consequently past growth (and the size achieved) may influence future growth (Beyer and Laurence 1980; Fuiman and Higgs 1997), we would also expect variability to increase in a multiplicative fashion, as was observed. Given that metamorphosis appears to be mainly cued by size (with age ensuing as a result of growth), a multiplicative effect of the environment on body size would predict a lognormally distributed metamorphic age (Wilbur and Collins 1973). Although the data to evaluate this directly were scarce, I believe that this is a plausible explanation because an important property of the lognormal distribution is that the mean and SD of a sample are linearly related (Aitchison and Brown 1976). The exponential relationship between age and SD observed here points to increasing skewing of the distribution as age increases, which may have important consequences to population-level survivorship. For a population with a given coefficient of variation in metamorphic age, if age is normally distributed there are approximately equal frequencies of larvae with better or worse chances of survival (i.e., each side of the mean), but a lognormal distribution implies that some individuals are disproportionately affected as the frequencies become skewed.

Another important consequence of the mean-SD relationship for metamorphic age is that it implies that individuals diverge in body size in a relatively predictable manner in time, regardless or taxonomy, habitat or growing conditions. The pattern also implies that some degree of serial autocorrelation (which causes the diversion) must exist in the performance of individuals (e.g., size-at-age, growth rate), such that relatively better developed individuals on one day are likely to be among the better developed in the cohort the next day. This type of autocorrelation also suggests that the timing of metamorphosis for individuals may be determined some time prior to its initiation, a result found by Bertram et al. (1997) for winter flounder.

The only conclusion that can be reached regarding metamorphic length and its variability is that intraspecific patterns do not conform well with those at the population level. This may result from a species-specific (relatively fixed) mean metamorphic size, which is affected by variability in growth rate or metamorphic age to produce the observed size variability. As an example, a comparison of dover sole (*Microstomus pacificus*), rex sole (*Glyptocephalus zachirus*) and petrale sole (*Eopsetta jordani*) which have a pelagic existence of over a year (or less), one year, and about six months respectively, showed that variability in metamorphic length was concomitant with stage duration (Pearcy et al. 1977). Mean metamorphic lengths were 19.3 mm, 61.3 mm and 18.5 mm, and coefficients of variation (calculated from their table 3) were 23.4%, 12.6%, and 10.0%, respectively (note that relative variability is used here rather than standard deviation as species with large differences in size are contrasted). Thus, longer stage durations mean that larvae have a greater amount of time to diverge from

one another in terms of body size. Furthermore, larvae with long pelagic existences may be more susceptible to dispersal, and to be exposed to different growth conditions. The interdependence of metamorphic age and length in determining variability in these traits is further corroborated by the observation that their respective mean-SD relationships had nearly identical slopes (1.435 and 1.456 respectively), although I cannot speculate on the origin of this dependence.

The goal of this review was to examine the scope for variability in the timing of metamorphosis in marine fishes, particularly for the level of the individual, where data had previously not been synthesized. Although the shape of the metamorphic age-standard deviation relationship allows us to infer the mechanism which results in the divergence of individuals in age at metamorphosis, experiments are needed to test the models of metamorphosis developed for amphibians (e.g., Wilbur-Collins, Leips-Travis, ontogenetic niche shift). Ultimately, the relative stability of metamorphic length within species may suggest that it is an adaptive trait, possibly determined as predicted by niche shift models (Werner 1986; Houde 1997a). The variability surrounding the mean ages and sizes suggests that individual timing of metamorphosis about these averages may be determined more subtly by individual growth trajectories. Bertram et al. (1997) have shown that age at metamorphosis in winter flounder begins to be established weeks before metamorphosis is initiated, by the size that larvae have achieved at that time. This result conforms with the Leips-Travis model of ontogenetic loss of flexibility in metamorphic age (Travis 1984; Hensley 1993; Leips and Travis 1994), but does not constitute a true test of either the Leips-Travis or Wilbur-Collins

models, as a single growing environment was used. Clearly more studies of individual timing of metamorphosis are needed, across a broader range of growing conditions, if we are to understand the constraints which occur at the level where mortality may be selective.

Given the potential for life history variability elucidated in this review, the next logical step is to determine if the end results of this variability are indeed important to survival for larval and juvenile marine fishes. Recent reviews with regard to survival during the early life of marine fishes have cautioned against invoking single factors (e.g., predation vs. starvation) to universally explain mortality, as little evidence exists to justify the dichotomies (Anderson 1988; Bailey and Houde 1989; Cushing 1990; Leggett and DeBlois 1994). Given that the various factors which can affect mortality (predation, starvation, disease, etc.) are not mutually exclusive, and can vary spatially, temporally, and among taxonomic groups, unifying theories are unlikely. Nonetheless, growth rate affects most of the selective mortality factors, through effects on both size-at-age and age-at size, as well as condition of larvae. Consequently, many agree that it is the interrelation of growth and mortality rates that affects recruitment as growth prolongs exposure to the various elements (Beyer 1989; Houde 1989a,b, 1997; Pepin 1991; Leggett and DeBlois 1994; Bell et al. 1995). The evidence found here for variability in metamorphic age resulting from growth rate variability across species, populations and individuals indicates that the effects of time can be of significant consequence in the differential survival of individuals as well differential population dynamics across stocks.

Table 2.1 Regression equations and correlation coefficients for various life history parameters, measured among species. Species with information on more than one population had each sample weighted by the inverse of the number of populations. The total number of populations is given as well as the number of species represented for each combination of parameters (mean growth rate (MG), temperature (T), length at metamorphosis (LM), age at metamorphosis (AM), hatching length (HL), standard deviation in metamorphic age and length (SD_{AM}, SD_{LM})).

Variables Regression Equation	Number of cases	Number of species	SE intercept	SE slope	r	Kendall's τ
Mean Growth (MG) and Temperature (T)						
log (MG) = -2.843 + 1.927 log (T)	62	12	0.207 ***	0.176 ***	0.82	0.61 ***
Length at Metamorphosis (LM)						
log (LM) = 1.083 - 0.148 log (HL)	226	43	0.033 ***	0.088 ns	-0.10	-0.18 **
log (LM) = 1.174 + 0.267 log(MG)	222	124	0.024 ***	0.042 ***	0.40	0.43 ***
log (LM) = 0.279 + 0.685 log (T)	62	12	0.130 *	0.112 ***	0.62	0.38 ***
Age at Metamorphosis (AM)						
log (AM) = 1.128 - 0.588 log (MG)	222	124	0.033 ***	0.056 ***	-0.58	-0.51 ***
log (AM) = 2.682 - 0.959 log (MG)	62	12	0.144 ***	0.123 ***	-0.71	-0.43 ***

Table 2.1 Continued

Variables	Regression Equation	Number of cases	Number of species	SE intercept	SE slope	r	Kendall's τ
Age - Length at Metamorphosis							
	log (LM) = 0.589 + 0.306 log (AM)	221	124	0.057 ***	0.039 ***	0.47	0.04 ns
	log (slope+1)[a] = 0.697 log(MG) - 0.099	28	7	0.008 ***	0.020 ***	0.99	0.77 ***
	SD ratio[b] = 1.087 (MG) - 0.076	28	7	0.030 *	0.078 ***	0.94	0.63 ***
Variability (SD) in Life History Parameters[c]							
	log (SD_{AM}) = 1.435 log (AM) - 1.670	187	137	0.099 ***	0.067 ***	0.84	0.70 ***
	log (SD_{LM}) = 1.456 log (LM) - 1.670	70	30	0.230 ***	0.207 ***	0.65	0.53 ***
	log(SD_{LM}) = -0.133 - 0.058 log (SD_{AM})	59	23	0.074 ns	0.147 ns	-0.05	-0.09 ns

[a] slope of length on age, within populations. Slopes were increased by 1, in order to eliminate non-positive values.

[b] SD ratio = SD_{LM} / SD_{AM}

[c] only taxa with 10 individuals or greater are included

*** P < 0.0001, ** P < 0.01, * P < 0.05, [ns] P > 0.05

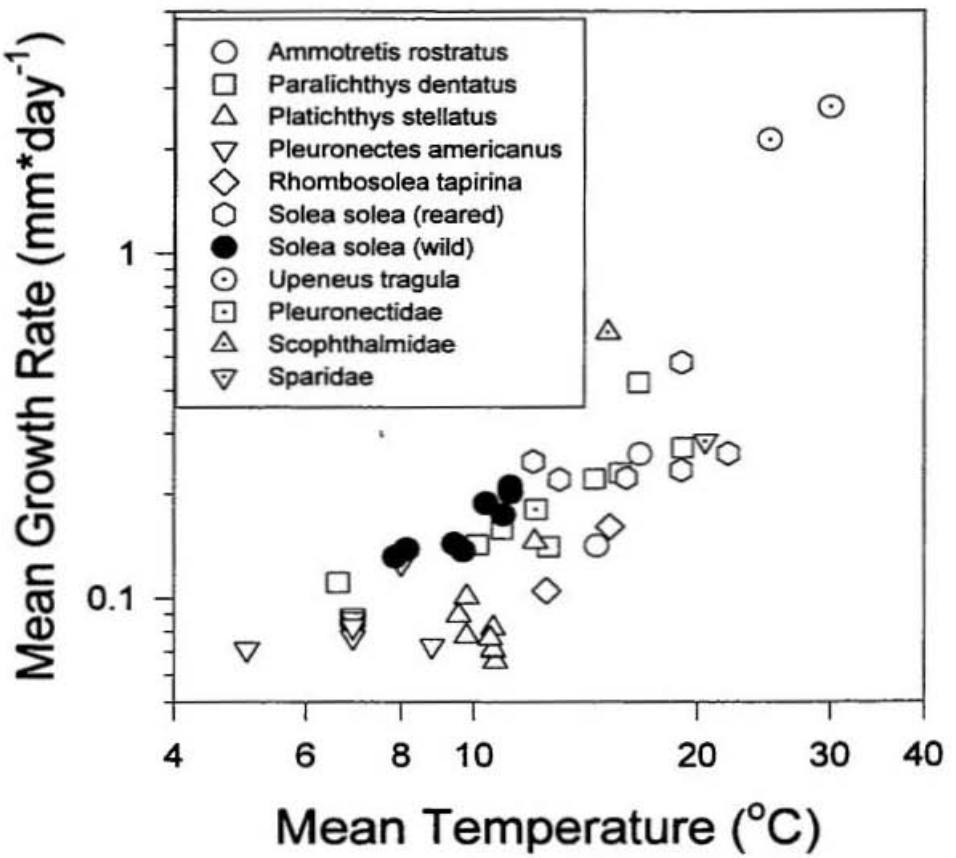


Figure 2.1 Interspecific and among populations (intraspecific) relationship between average temperature (°C) and average growth rate (mm•day^{-1}), for reared and wild larvae. Species for which information was only available for one population are grouped according to Family (in order to minimize clutter) . Note the logarithmic axes.

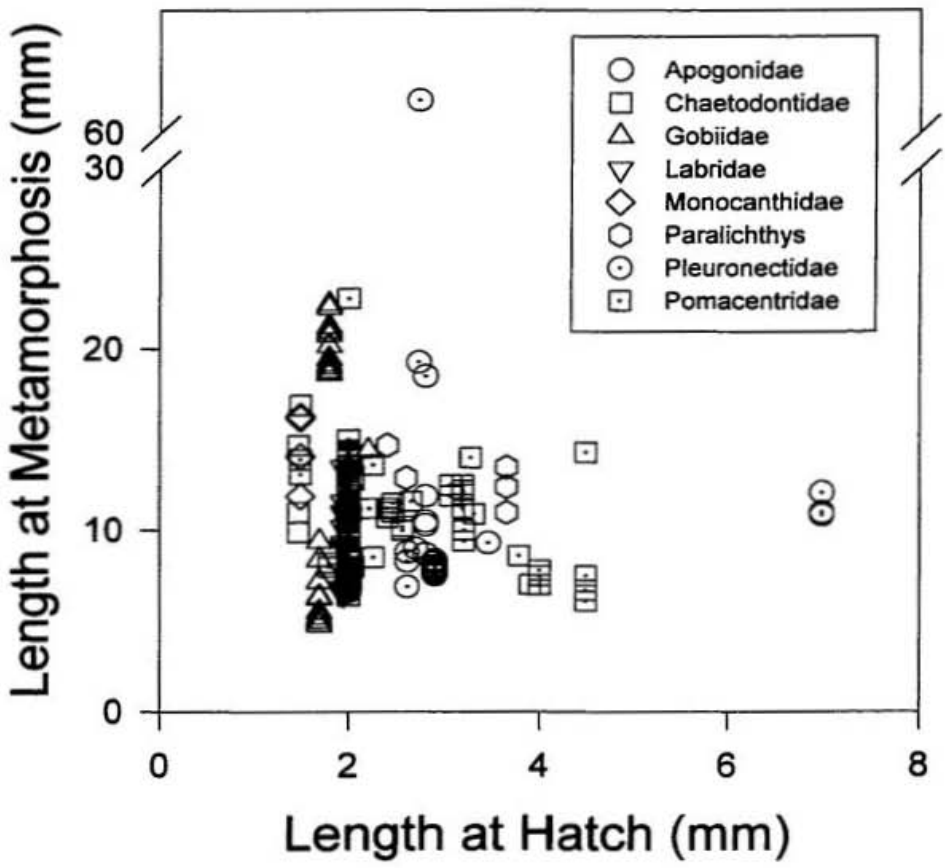


Figure 2.2 Relationship between lengths (mm) at hatch and at metamorphosis at the Family level (there were too many species to graph them individually). Only Families with more than two species are presented in the graph. Note that only species for which a species-specific hatch length was available are included.

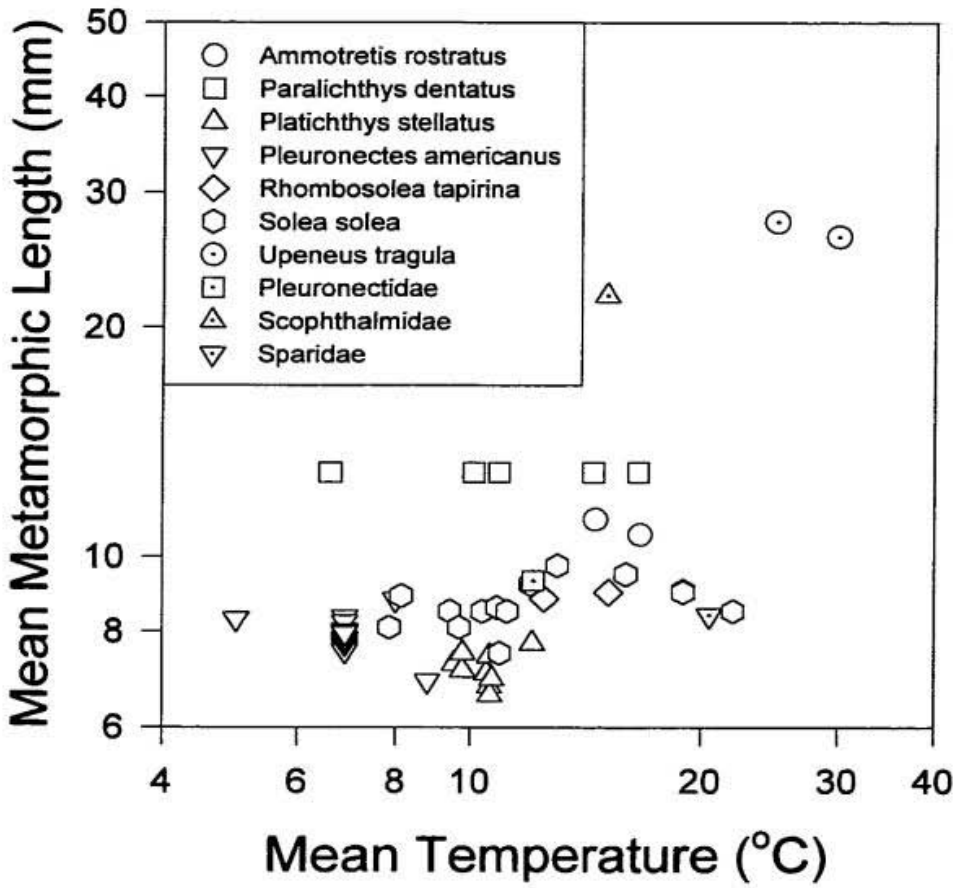


Figure 2.3 Interspecific and among-populations relationships between average temperature (°C) and average metamorphic length (mm). Species for which information was only available for one population are grouped according to Family. Note the logarithmic axes.

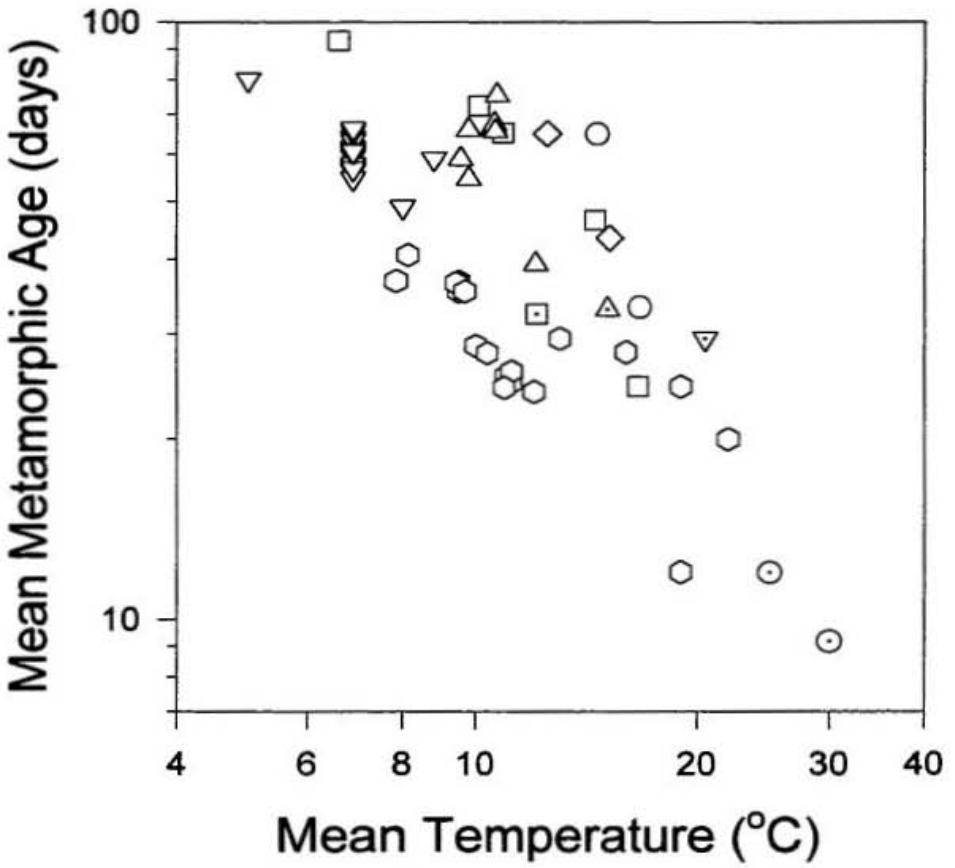


Figure 2.4 Interspecific and among-populations relationships between average temperature (°C) and average metamorphic age (days). Refer to the legend in Figure 2.3 to identify the symbols. Species for which information was only available for one population are grouped according to Family. Note the logarithmic axes.

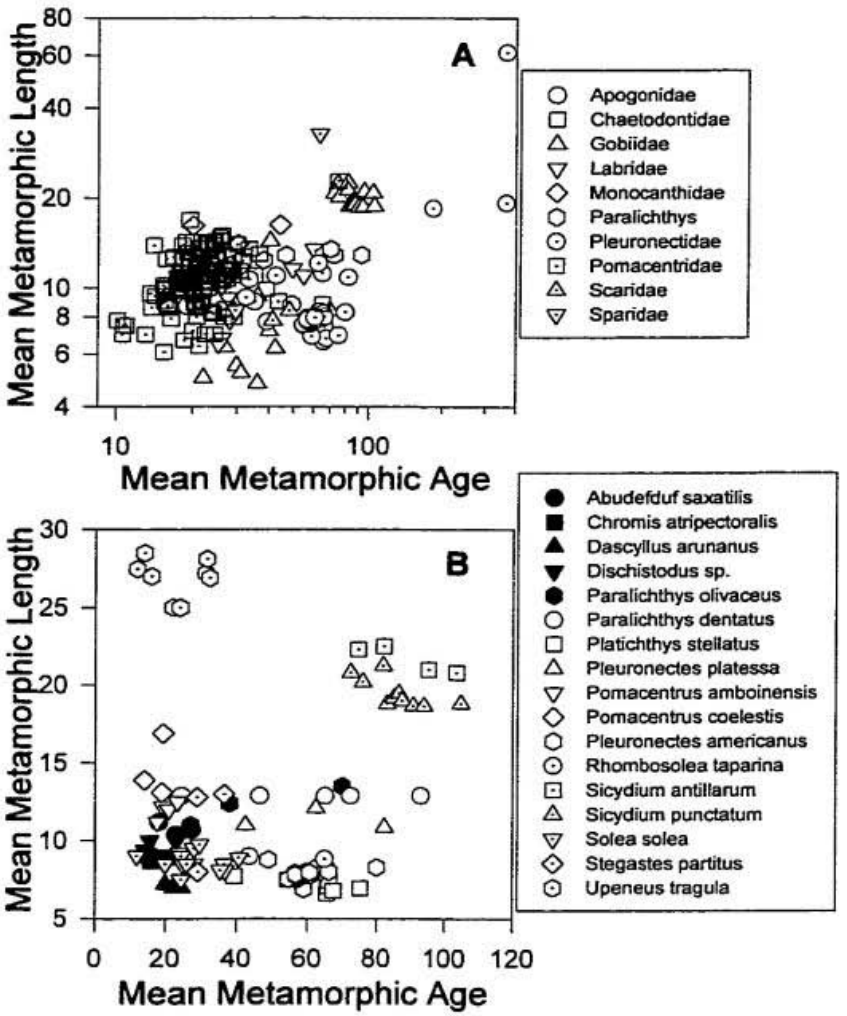


Figure 2.5 (a) Interspecific relationship between average metamorphic age (days) and length (mm) grouped according to Family. Note the logarithmic axes. (b) Among populations relationship between average age (days) and length (mm) at metamorphosis. Only taxa with three or more populations are included in this figure in order to minimize clutter.

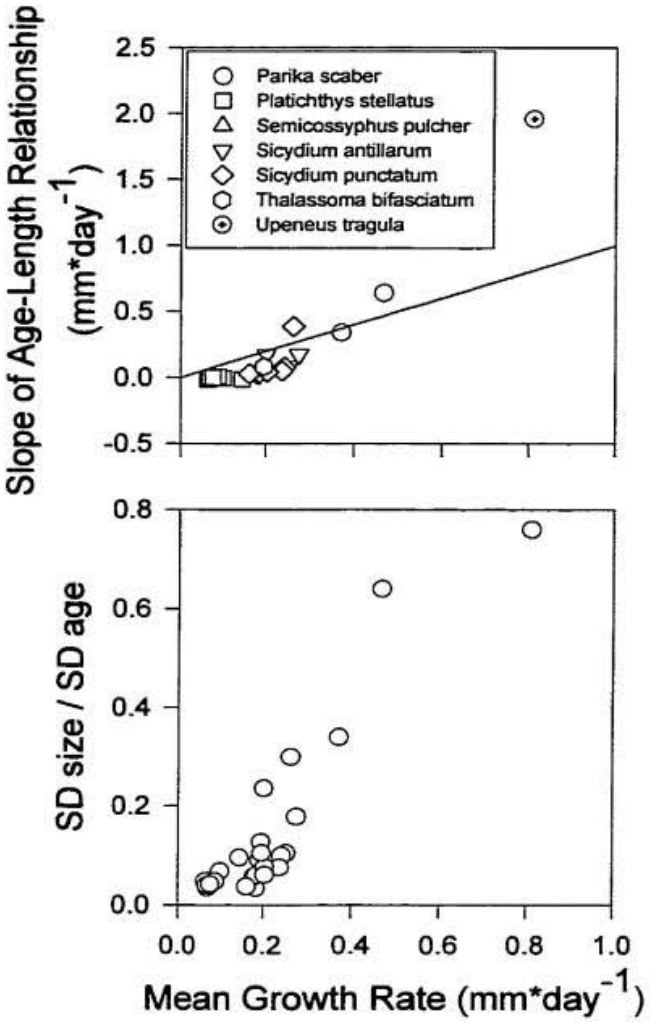


Figure 2.6 (a) Interspecific and among-population comparisons of the population level metamorphic age-length slope, and average growth rate (mm•day^{-1}). Although analyses are performed on log-transformed data, the untransformed relationship is shown here to emphasize the deviation from a 1:1 relationship (solid line), (b) Relationship of mean growth rate (mm•day^{-1}) to the relative variability in length versus age at metamorphosis (the ratio of the standard deviation of length and that of age).

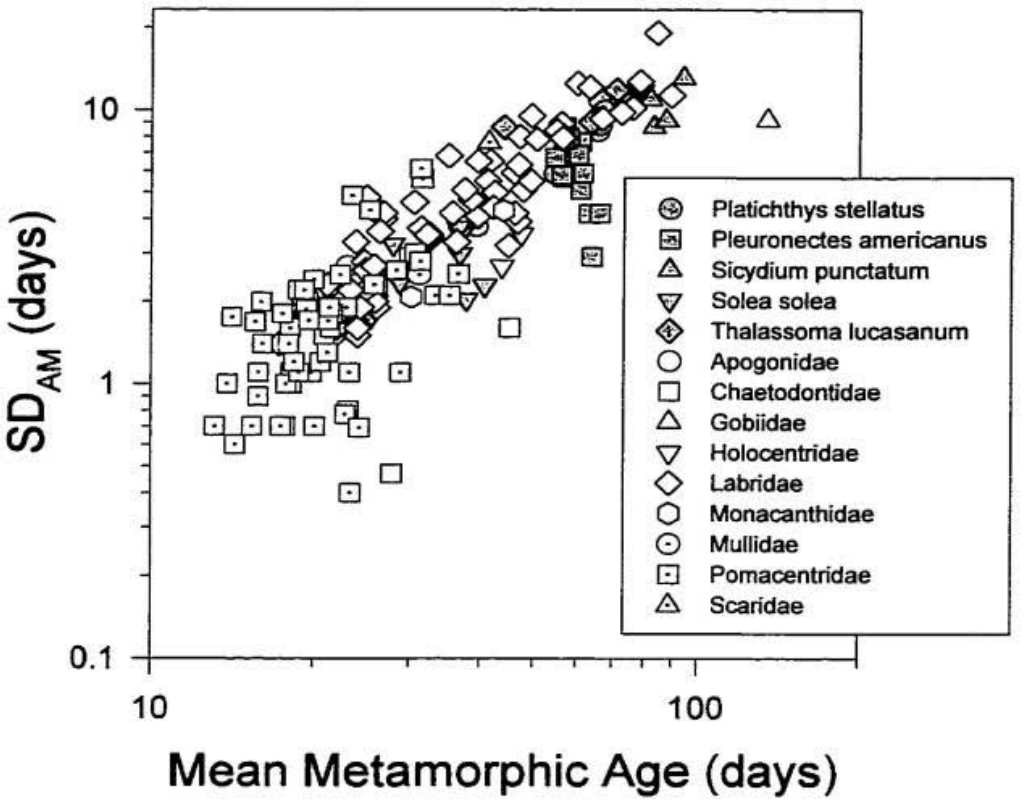


Figure 2.7 Interspecific and among populations relationships between mean metamorphic age (days) and SD_{AM} (days), for populations with 10 or more individuals in the sample. Species for which information was only available for one population are grouped according to Family. Note the logarithmic axes.

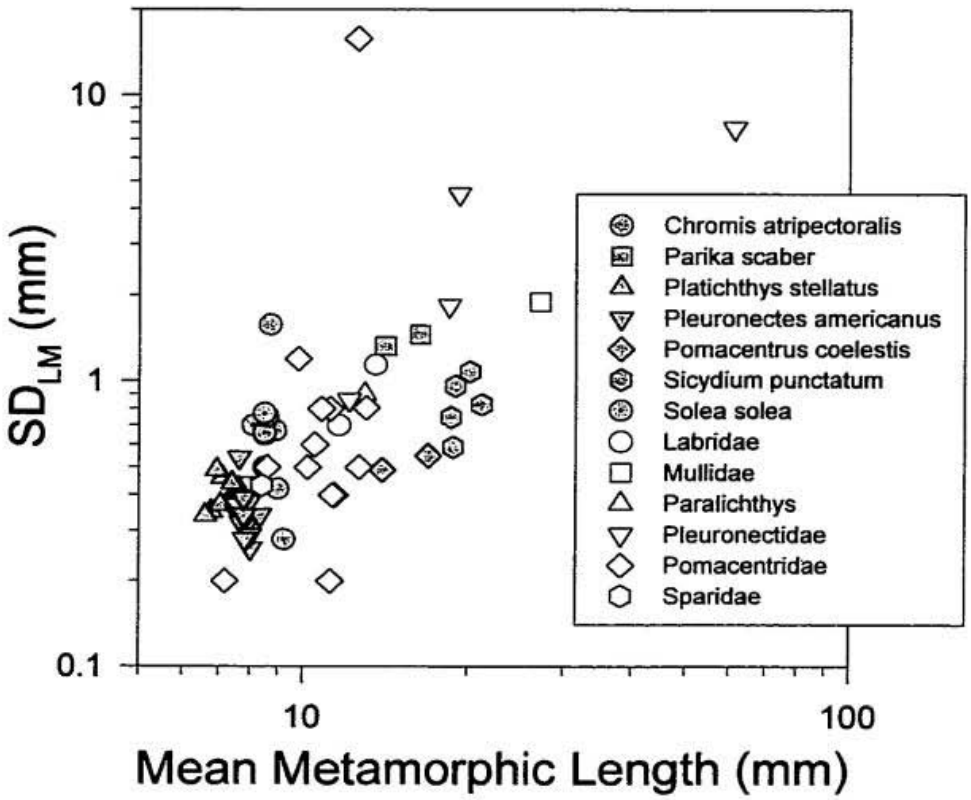


Figure 2.8 Interspecific and among populations relationships between mean metamorphic length (mm) and SD_{LM} (mm), for populations with 10 or more individuals in the sample. Species for which information was only available for one population are grouped according to Family. Note the logarithmic axes.

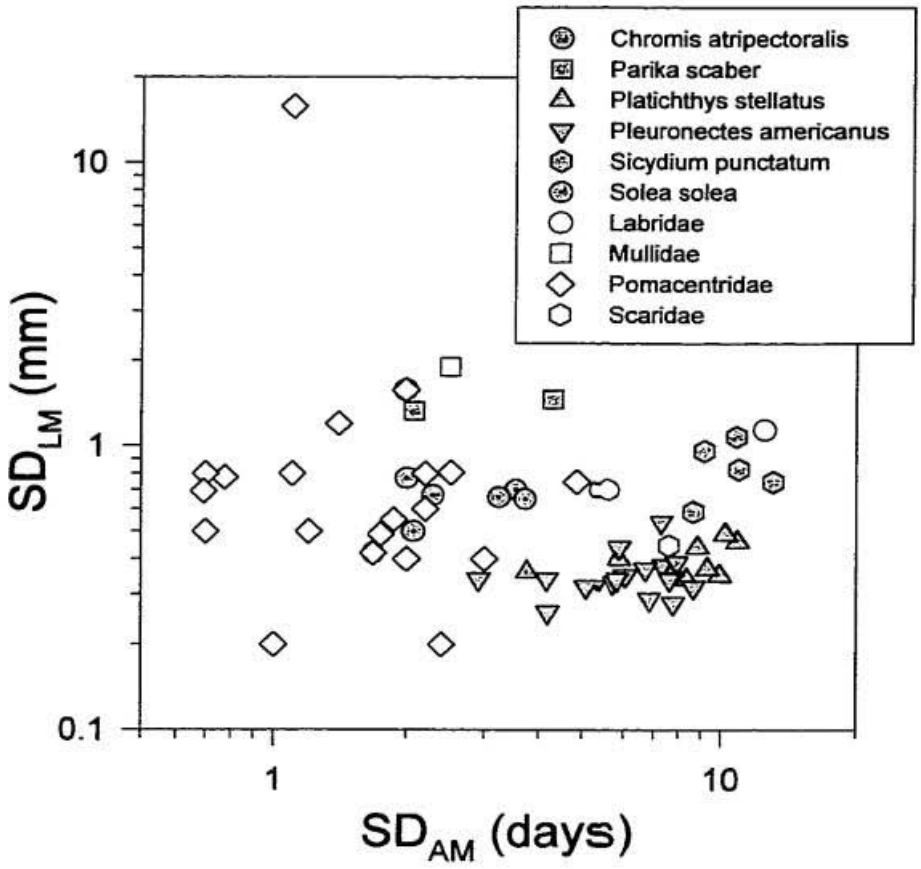


Figure 2.9 Interspecific and among populations relationships between SD_{AM} (days) and SD_{LM} (mm) for populations with 10 or more individuals in the sample for each measure. Species for which information was only available for one population are grouped according to Family. Note the logarithmic axes.

Chapter 3

Individual variability in growth rate and the timing of metamorphosis in yellowtail flounder, *Pleuronectes ferrugineus*

Abstract

The individual-level variability in growth and development rates of yellowtail flounder (*Pleuronectes ferrugineus*) larvae, and its impact on age and size at metamorphosis was studied. Larvae were reared from hatch to metamorphosis in three separate temperature treatments. Temperature influenced the location and distribution of individual transition ages and lengths of larvae reared in separate aquaria. This was mainly due to the influence of temperature in determining the mean and range of individual growth rates in a treatment. Individual metamorphic ages were negatively correlated with the growth rate of larvae. Individual metamorphic lengths generally increased as mean individual growth rates increased, but higher mean growth also resulted in a wider diversity of lengths. In one of the treatments the otoliths of the larvae were stained three times during the larval period using alizarin complexone, allowing me to reconstruct the growth history of individuals once they had metamorphosed. The body length that larvae had achieved by two weeks after hatch correlated negatively with the eventual age at metamorphosis. This relationship became stronger the nearer larvae were to metamorphosis. These results were attributed to serial autocorrelations in body length, and to a lesser extent growth rate, for individuals during the larval period. Overall these results suggest that events occurring early during ontogeny, that affect the

size and growth rates of larvae, can impact life history transitions occurring several weeks or months later.

Introduction

During the early life history of the majority of fish, body size increases by orders of magnitude and adult characters are acquired within weeks. Meanwhile, eggs and larvae suffer high mortality rates (Dahlberg 1979; Sissenwine 1984). Recruitment begins to be roughly established at the late larval or early juvenile stages (Bradford 1992), when the biomass of the cohort ceases to decrease as a result of mortality, and begins to increase due to the growth of individuals (Beyer 1989; Houde 1997b).

Which factors control recruitment in marine fishes is unclear (for reviews see Anderson 1988; Bailey and Houde 1989; Cushing 1990; Leggett and DeBlois 1994), however growth is important in determining overall survival. Differences in development and growth rates will affect the age-at-size, size-at-age and timing of early life history transitions (hatch, first feeding, yolk absorption, metamorphosis) (Chambers et al. 1988; Bertram et al. 1997), and consequently may determine which individuals survive (Litvak and Leggett 1992; Pepin et al. 1992; Bell et al. 1995). Physiological (capacity for metabolism and catabolism) and environmental (temperature, food availability) factors affect transition size and age (Pepin 1991; Chambers and Leggett 1992, 1996; Chapters 2 and 4). Subtle differences in the timing of transitions, which often include large changes in behaviour, morphology, habitat and niche can potentially

create large changes in recruitment, with metamorphosis likely being the most important (Houde 1987, 1989b; Beyer 1989; Pepin and Myers 1991; Bell et al. 1995).

Among species and populations, metamorphosis appears to be centered around a relatively fixed length, and transition age varies as a consequence of growth variation (Houde 1989a; Chambers and Leggett 1992; Chapter 2). Among species, population level standard deviation in both age and length at metamorphosis increases exponentially with increases in their respective means (Chapter 2). This suggests that the variance-generating mechanism is similar for all marine fishes regardless of their environment. A nearly identical power law (log-log mean-variance relationship) for metamorphic age and length further suggests that the two are not independent and that a "target" transition length may not be an appropriate model for the timing of metamorphosis at the individual level. This is further supported by the observation that the strength of the metamorphic age-length relationship among individuals is directly proportional to the mean growth rate (Chapter 2).

The role of the environment and its interaction with genetic and non-genetic parental contributions (Chambers and Leggett 1989b, 1992; Chapter 4) in determining the traits of individuals is generally poorly understood (e.g. Policansky 1982). This remains a problem because the majority of studies that have reared fish to metamorphosis under a variety of growing conditions fail to report the effects on the dispersion and distribution of traits within populations (e.g. Laurence 1975; Fonds 1979; Crawford 1984; Seikai et al. 1986). Understanding of the timing of metamorphosis at the individual level is essential because any selective mechanisms

affecting survival and recruitment will ultimately operate at that level (Sharp 1987; Crowder et al. 1992; Rice et. al 1993).

In this study I quantify variation in age and size at metamorphosis in cohorts of yellowtail flounder (*Pleuronectes ferrugineus*), and describe how this variation changes with the growing conditions. This direction follows from the idea that variance among individuals in the timing of metamorphosis is generated in a predictable and continuous manner, which is likely a result of individual variation in growth rates (Chapter 2). To explore the idea that individual differences in larval growth trajectories are responsible for generating this variance, I also reconstruct the growth history of individuals, using the otoliths of metamorphosed fish. This allows me to determine when individual metamorphic traits (ages and sizes) become predictable by the size that larvae have achieved at an earlier date.

Methods and materials

Laboratory growth rate of larvae was manipulated by altering the temperature at which they were reared. I chose this approach rather than manipulating food availability in order to minimize the problems associated with food deprivation, which can result in competition among individuals and affect the physiological condition of larvae. Because the objective was to focus on how variation in growth rate during the larval period affects the timing of metamorphosis, eggs were reared to hatching under identical conditions (8.4°C) and acclimatized to larval rearing temperatures after hatching.

Six, 225 L temperature-controlled water baths were used to create three treatments (2 baths per treatment) at nominal temperatures of 7° (7.3±0.1 °C, mean ± SD), 11° (11.1±0.2 °C), and 13°C (13.2±0.2 °C) in which larvae were reared. Three or four (20 L, 20cm x 40cm x 25cm) aquaria were placed in each bath, for a total of seven per temperature treatment. The outside walls of the aquaria were covered with black plastic to enhance the contrast of prey items for the larvae. The aquaria were filled with 18 L of UV sterilized filtered sea water, and rearing conditions were kept static except for partial water changes (3-4 L) every three days during the egg stage and every two days during the larval stage. Dead eggs or larvae and detritus were siphoned from the bottom of the tanks during water changes. A 17-hour light, 7-hour dark photoperiod, representative of the natural photoperiod, was maintained using florescent lights hung approximately one meter above the tanks. Temperatures were measured three times daily (at approximately 9:00, 13:00, 17:00) using a digital thermometer, with 0.1 °C accuracy. Temperatures varied little and the time series of temperature were deemed stationary (no long term trends or cycles) by visual inspection.

Yellowtail flounder eggs were obtained by stripping six females from a broodstock held for 2-3 years at the Ocean Sciences Center, Memorial University of Newfoundland (Canada). An equal contribution of eggs from each female was used to create a pool of mixed eggs. An aliquot of 4.0 mL of eggs (yielding ~9140 ± 340 eggs) was placed into each of twenty-one 20-mL plastic vials that were placed in an 8.4°C bath for 20 minutes. After acclimation, fertilization was performed by mixing 0.2 mL of mixed sperm (from 5 males) with the eggs. A mixture of gametes from several

parents was used to randomize possible parental effects within and among treatments. Filtered sea water (5 mL) was added to the vials in order to activate the sperm. After two minutes the fertilized eggs were gently poured into each of the 28 aquaria containing 18 L of UV-sterilized filtered seawater.

Fertilized eggs were kept at 8.4±0.2°C throughout the incubation period. At the first water change, 100 mg•L^{-1} of Streptomycin and 60 mg•L^{-1} of Penicillin were added to the tanks. Eggs began hatching six days after fertilization with median hatch occurring on the seventh day. On the ninth day after fertilization, 25-40 larvae from each aquaria were removed and measured for standard length under 250x magnification using an imaging system (Bioscan OPTIMAS® 4.10), in order to establish the initial size distribution of larvae. To minimize disturbances, eggs, and subsequently larvae, were reared in the same aquaria. Beginning on the ninth day, temperatures were slowly changed (1°C•day^{-1}) to establish the three separate temperature treatments (7, 11, 13°C). In addition, 0.5 L of golden algae (*Isochrysus* sp.) along with very light aeration were added to each aquarium. Aeration was subsequently increased 2 weeks later when a second antibiotic treatment was given to the larvae.

Larvae were fed *ad libitum* throughout the experiment. Cultured rotifers (*Brachionus* sp.) enriched with a mixture of powdered media and fresh algae were used throughout the experiment, although the size of rotifers added to the tanks depended on the size of the larvae. The average size of rotifers added to the aquaria was increased over the larval period by screening the rotifers using a nylon sieve. Rotifers measuring 40-120 μm were added twice daily at densities of 4.0•mL^{-1} beginning one week after

hatching. Once average larval size reached 4-5 mm, mean rotifer size was increased by using only animals >100 μm. For larvae between 5-6 mm, rotifers were selected using a 150 μm mesh. In addition to rotifers, brine shrimp (*Artemia* sp.) were added in densities of 2.0•mL^{-1} once larvae reached an average of 7-8 mm. Densities of brine shrimp were increased to 4.0•mL^{-1}, and rotifer densities decreased to 2.0•mL^{-1} approximately one week later.

As larvae approached metamorphosis, individuals were examined every second day in order to find those that had metamorphosed. I defined metamorphosis as the point at which the iris of the migrating eye reached the neural crest, and was visible from the other side of the body. This is commonly used as a standard method of scoring metamorphosis (e.g. Chambers and Leggett 1987; Bertram et al. 1997). Metamorphosed individuals were removed from the aquaria, killed and preserved in 95% ethanol. To assess the effect of preservation on body measurements, standard length and maximum body diameter (measured perpendicular to the longest axis of the fish) were measured on >350 live individuals under 64x magnification. These individuals were re-measured 3-4 months later (when all metamorphosed fish were measured). Age at metamorphosis is defined as the number of days between scoring a fish as a metamorph and modal hatching date.

Experiments were terminated prior to metamorphosis for 4 fish at 7°C. The larvae were nonetheless measured and their development was roughly scored by the

position of their migrating eye. These individuals were included in some of the analyses that are able to accommodate such data (see *Analysis* section for details).

Individual growth histories

Given the inability to tag individual larvae, and the difficulty in rearing individuals in isolation to make repeated length measurements (see Bertram et al. 1997), I chose to utilize the relationship between body length and otolith diameter of common age fish to reconstruct the growth history of individual fish. In order to alleviate problems associated with non-daily deposition of otolith rings (e.g. Sogard 1991; Szedlmayer and Able 1992) and variation in the otolith:somatic growth relationship (Campana 1990), I marked the larval otoliths at specific time intervals in the 11°C treatment. I could then confidently measure the diameter of the otolith at that time and back-calculate the size of the fish. I used a solution of seawater and alizarin complexone ($C_{19}H_{15}NO_8\,H_2O$), which is incorporated into new otolith growth increments and fluoresces under UV-light. Otoliths were marked on the 18th, 30th and 43rd day of the larvae period in 3 of the 7 tanks in the 11°C treatment (Table 3.1).

To mark the larval otoliths, the water volume in the three aquaria was reduced to 5 L. Four liters of a 112.5 $mg \cdot L^{-1}$ alizarin solution (prepared by diluting 1.35 g of alizarin in 270 mL of distilled water and topping up with 11.7 L of seawater containing algae and rotifers) was gently poured into each aquarium to yield a final concentration of 50 $mg \cdot L^{-1}$. Immersion of larvae lasted 16 hours, after which they were transferred using a nylon filter to aquaria containing filtered seawater and algae. Overall the

staining process and subsequent transfer of larvae to clean water resulted in very low mortality (<3 individuals per tank per staining period).

These aquaria were checked for metamorphosing larvae in the same manner as unmarked treatments, and individuals were preserved similarly. After measuring for preserved length, left and right otoliths (sagitta, lapilli and asteriscii) were removed using a dissecting scope and mounted on microscope slides using thermoplastic cement. Lapilli were viewed under 1000x magnification using 365 nm UV light and a wide band interference blue filter. The diameter of each fluorescent ring and the total diameter of the otolith were measured along the longest axis using an ocular micrometer. Fluorescent bands did not appear on the asteriscii, likely because these form later during ontogeny (Secor et al. 1992). Sagittae had large accessory primordia, that appear to form once metamorphosis begins (*personal observation*), and that would have required substantial polishing in order to measure the bands.

In order to establish the relationship between otolith diameter and larval length for each staining period, 10-15 larvae were removed from each of the "stained" tanks the day following each marking, and were measured and preserved individually in ethanol. The otoliths from these larvae (lapilli and sagittae) were later removed, mounted and measured as described above. Unfortunately the larvae that were taken for the 18 and 30 day staining periods were preserved in ethanol that was too weak (<80%) and consequently became too acidic to properly preserve the otoliths. I later obtained 11 and 20 day old larvae from two separate general rearing stocks held at the Ocean Sciences Center (Memorial University) that had similar mean lengths as the

larvae from the experiment at 18 and 30 days respectively, in order to establish otolith diameter:body length relationships. There is the potential that different growth rates of these larvae would result in differences in the slope and intercept of the relationship (Reznick et al. 1989; Campana 1990). In order to avoid introducing any biases in my data, all analyses were performed using otolith diameters rather than back-calculated body lengths. Growth rates were calculated as the increase in otolith diameter (μm) divided by the time interval over which growth was measured. Growth rate from hatch to day 18 was calculated assuming a constant diameter of 11 μm at hatch (estimated from the diameter:length relationship for the youngest larvae, and assuming a mean hatching length of 3.2 mm). Analyses involving otolith diameters and growth rates were performed using rank correlations (which are independent of absolute magnitude).

Analyses

Covariance between age and length at metamorphosis among individuals was analyzed using nonparametric correlation analyses (Kendall's τ), which assumes a monotonic relationship between variables, in addition to segmented regression analysis that fits a biphasic regression to the data. A nonlinear, segmented fitting algorithm (Wilkinson 1992) was used to test the working assumption that the data can be represented by two linear segments, differing in slope. In particular, I was interested in determining non-arbitrarily a point at which age and length at metamorphosis go from being uncorrelated to being positively related. The model used was of the form:

(1) length = $B_0 + B_1$(age), when age $\leq$ BREAK

length= $B_0 + (B_1 + B_2)$(age), when age > BREAK

B_0 is the intercept (mm), B_1 is the slope of the first segment (mm•day^{-1}), B_2 is the difference in slope between the first and second segment (i.e. the slope of the second segment = B_1+B_2), and BREAK (days) is the inflection between the first and second segments. Confidence intervals (95%) are reported for each parameter. I acknowledge that the relationships to which I fit the lines are continuous, but as mentioned previously, I was most interested in determining the location of a possible break point, rather than testing hypotheses on the magnitudes of the slopes or describing the functional relationship in detail. I only fit biphasic regressions to data from those tanks that visually showed a change in age-length correlation over time. Robustness of parameter estimates was tested by varying the initial values used in the estimation.

The analyses of the frequency distributions of both age and length at metamorphosis were performed using event analysis (Cox and Oakes 1984; Chambers and Leggett 1989b), in which the entire distribution of ages or lengths is used to describe the timing of metamorphosis. One advantage of this technique over standard parametric analyses, which compare average responses and use variance as a description of error, is that information from all individuals in the population is retained at its original level, rather than amalgamating it in the estimation of a mean. A second advantage is that this type of analysis allows the incorporation of data on individuals that were removed from the experiment prior to undergoing the event (termed "censored" individuals). This reduces potential biases because until the individuals

were removed from the experiment, they were at "risk" of undergoing the event, and consequently they contribute to the dispersion.

A Weibull distribution was used to model ages and lengths at metamorphosis as it provided the best log-likelihood fit to the data. The survival function of the Weibull distribution is defined as

(2) $S(t) = \exp[-(t / \alpha)^{\gamma}]$

where t is the timing of the transition (i.e. age or length at metamorphosis), α is a scale parameter in units of time (days) or length (mm), and γ is a dimensionless shape parameter. The survival function is the complement of the cumulative frequency distribution [$F(t)$] of metamorphic ages and lengths (i.e. $S(t) = 1 - F(t)$). Equation (2) can be modified into an accelerated failure time model by including 'n' treatment variables (e.g. temperature, fish density, etc.), described by a vector $v' = (v_1, v_2, ..., v_n)$, such that

(3) $S(t; v) = \exp[-(t / \alpha)^{\gamma} \exp^{v'\beta}]$

assuming that the elements of v interact through a linear function, $v'\beta$, where β_i are parameters to be estimated.

The analysis uses log-transformed ages or lengths, which yields the standard extreme value distribution that is multiplied by a scale factor (analogous to the variance of a normal distribution), and translated by a location parameter (~mean). Observations of individual event times are related to explanatory variables in a regression model, as

(4) $Y = V\beta + \sigma \varepsilon$

where Y is the vector of log-transformed ages or lengths at metamorphosis, V is the matrix of explanatory variables, β is the vector of coefficients to be estimated, σ is the scale parameter to be estimated, and ε is the extreme value distribution in the case of the Weibull distribution. Sigma (σ) is the inverse of the shape parameter γ in the Weibull distribution, and β_1, an estimate of the intercept, is the location parameter of the extreme value distribution (i.e.= $\log(\alpha)$). Finally, ε is a random error vector from the assumed extreme value distribution. In equation (4) the explanatory variables act multiplicatively on individual ages/sizes, resulting in acceleration of event timing. Parameters were estimated using iterative maximum likelihood methods.

Results

Overall, survival was variable across aquaria and temperatures (Table 3.1). As a result only five tanks were available for analysis at 7°C, with generally low numbers except in one tank. At 11 °C survival was variable across replicates but sample sizes in all aquaria were high. Due to an accident in the 13 °C treatment two months into the study, all but one replicate were lost. As a result of this variability I will include all of the aquaria in a general analysis of temperature or growth effects, but I will subsequently focus on the 11 °C treatment to assess sources of experimental error among replicates.

Effects of preservation

Preservation in 95% ethanol caused substantial shrinkage of the metamorphosing larvae. Preservation effects were estimated by fitting an asymptotic relationship to data from 371 fish, where

(5) preserved length = β_o (1 - exp(-β_1•fresh length))

where β_o is the asymptote of the curve, and β_1 determines the rate at which the asymptote is reached. This model performed very well (R^2=0.96, P<0.0001), with estimated parameter values and associated asymptotic standard errors of β_o=161.03 ± 26.14 and β_1=0.0061 ± 0.0011 (due to the high degree of explained variance I do not present a plot of these data). Preservation effects were also estimated for measurements of body depth (β_o=43.47 ± 6.93, β_1=0.025 ± 0.004, R^2=0.89, P<0.0001). The high degree of explained variance suggests that differential shrinkage of larvae (resulting in changes in the size rank of larvae) did not significantly affect my results regarding the statistical distributions of metamorphic lengths. All subsequent analyses have been performed using preserved lengths as the unit of study.

Covariation between age and length at metamorphosis

Mean age and length at metamorphosis were negatively correlated across tanks (n=13, r =-0.85, P<0.0001) (Figure 3. 1). The relationship is independent of temperature, suggesting that the average response of a population of larvae is a result of

the mean growth rate. Slower growth results in increased age and decreased length at metamorphosis.

Within aquaria the relationship between age and length is complex (Figure 3.2). In general there is little or no covariation between age and length in treatments with survivor numbers less than 85 individuals per tank (Table 3.1). Some exceptions occurred for tanks at 7 °C but these appear to be driven by relatively few older larvae (>140 days of age) (Figure 3.2). In contrast, a positive covariance develops in tanks with higher densities (Table 3.2, Figure 3.2). In tanks 1, 3, 4 and 6 of the 11 °C treatment a positive correlation between age and length at metamorphosis appears after an average of 89.0-97.9 days, as determined by segmented regression analysis (Table 3.2). By that time almost all of the larvae in the lower density tanks (#2, 5 and 7) had undergone metamorphosis, and consequently do not show this tendency.

Age at metamorphosis

It is difficult to describe the distributions for the raw data on metamorphic age beyond the mean and variance (Figure 3.2). Nonetheless, Weibull distributions fit reasonably well to observed distributions. Event analysis reveals that age at metamorphosis differed significantly among temperature treatments (Table 3.3), and a significant effect of fish density was also detected. Age at metamorphosis increased as temperature decreased and as the density of fish at metamorphosis increased.

Variance in age at metamorphosis was not significantly related to average age, as determined by a power law, or log-log linear regression ($F_{1, 12}$=2.13, P>0.1,

R^2=0.15), contrary to the findings presented in Chapter 2 for other species. As noted previously, event analysis had suggested that larval density affected age dispersion, consequently its effect was added to the linear model relating mean and variance. Although this increased the explained variance to 48%, all parameters were not statistically significant at α=0.05. Density did however significantly affect the skewness of the age distribution for untransformed data (r=-0.73, P<0.007, n=12), with lower density populations showing positive skewness and high densities resulting in slight negative skewness (Figure 3.3).

Length at metamorphosis

Event analysis shows that length at metamorphosis differed significantly among the 7°C and the 11 and 13 °C treatments, but the latter two did not differ significantly from one another (Table 3.3). A significant effect of larval density was also detected. Overall, length at metamorphosis decreased with decreasing temperature and with increasing density. Given the strong density effect at 11 °C, I explored the impact of larval density on the length distributions within each temperature treatment. Furthermore I incorporated the covariance with age to explore its effect on shaping the distributions of length within each treatment, as the segmented regression analysis had shown that this effect was not constant across aquaria and temperatures. The intercept, or location of the distributions, increased as temperature increased (Table 3.4). Age did not significantly affect the distribution of sizes at 7 °C, but had a significant impact in the other two treatments, although the effect at 13 °C is largely due to a few individuals

(Figure 3.2). The effect at 11 °C reflects the unequal distribution of ages among lengths (largest individuals also oldest) at higher densities. Density effects were marginally insignificant at 7 °C but highly significant at 11 °C (Table 3.4). Density effects at 11 °C were largely manifested in a shifting of the mode of the distribution towards smaller sizes as density increased, as the absolute range of sizes was relatively constant across aquaria (Figure 3.2). This effect of density on the mode of the distributions contributed to a significant positive relationship between density and skewness in length ($r=0.84$, $P<0.0001$, $n=13$) when all tanks/temperatures are considered (Figure 3.4).

A statistically significant power law, relating log-transformed mean length and its associated variance, explained 52.7% of the variance in the dispersion of lengths (slope=3.66±1.00 (SE), intercept=-3.85±1.24, $F_{1,10}=13.38$, $P<0.005$). Larval density had no significant effect on dispersion ($F_{1,10}=1.90$, $P=0.20$). This result further supports the observation that density affects mainly the skewness of the distribution of individual characters, without greatly affecting the range and dispersion of the lengths in a population.

Body depth

Length of metamorphosing larvae explained 87.6% of the variance in body depth in a log-log regression ($F_{1,1029}=2578$, $P<0.0001$). Expanding the linear model, I found a significant tank (nested in temperature) effect ($F_{16,1003}=15.22$, $P<0.0001$), although both temperature and length*temperature interaction effects were not significant ($F_{3,1003}=1.16$, $P>0.3$, and $F_{3,1003}=1.93$, $P>0.1$ respectively). Despite the

significant tank effect, the larger model only increased the explained variance by 3.6%. This result means that overall, body depth (a proxy for the weight of individuals) at metamorphosis did not significantly vary independently of metamorphic length. Furthermore, the lack of significant interactions between body depth and temperature suggests that weight scales to length in the same manner under different growth regimes (i.e. individuals are not growing in length at the expense of body mass).

Otolith reconstruction

Length corresponds reliably to otolith diameter in common aged fish as small as about 5 mm (Figure 3.5). Although the larvae from the two youngest groups were grown under different conditions than the experimental fish, they nonetheless fit in with the overall trend of increasing otolith diameter with increasing body size. This allows me to use otolith diameters for 18 and 30 day old experimental larvae as indices of larval length (i.e., we can assume that a relatively larger otolith came from a larger larvae, but we cannot estimate a length precisely). Overall the correspondence between otolith diameter and body length improves as mean length and the range of lengths increases, as suggested by decreasing standard errors and increasing explained variance (Table 3.5, Figure 3.5). The relationship at metamorphosis is weaker (Table 3.5), likely due to the diversity of ages-at-length, which can affect the otolith diameter: body length relationship (Reznick et al. 1989; Campana 1990).

The relationship between measured diameters for left and right otoliths of experimental fish improved as the larvae aged and grew (Table 3.5). For 18 day old

larvae, the diameter of the left otolith explained 64% of the variance in that of the right, which is likely a result of measurement error for small otoliths, in addition to the limited range of diameters being compared. Explained variance increased as did the slope of the relationship (tending towards a value of 1) for 30 and 43 day old larvae. Explained variance decreased slightly for the total diameter measured at metamorphosis, partly due to increasing deformities on the lapilli caused by the formation of small primordia (*personal observation*). For the analyses that follow, one of the otoliths was randomly chosen when measurements were made on both right and left otoliths.

A significant negative correlation between otolith diameter (~body length) and age at metamorphosis was detected for all aquaria at 18 days (Table 3.6, Figure 3.6). The correlation improved as larvae aged, and by 43 days otolith diameter explained about 38-74% of the variance in age at metamorphosis, a result similar to that found by Bertram et al. (1997). However, as I noted before, the relationship between age and length at metamorphosis was weak in tanks 2, 4 and 7 (Figure 3.2). To gain a better understanding of this result, I correlated the residuals from the age vs. size-at-43 day relationship, to the size at metamorphosis (Figure 3.6 d). By doing so I effectively separate age at metamorphosis into that which is due to the growth rate up to 43 days and that due to the deviation (residuals) from the metamorphic age that would be predicted from that relationship. The significant positive correlation between length at metamorphosis and "residual" age at metamorphosis in tanks 2 and 4 (and for the data overall) (Table 3.6) suggests that larvae that undergo metamorphosis sooner than would

be predicted from their size at 43 days (negative residual) do so at a size that is smaller than the overall average of 18.2 mm. On the other hand, those larvae that took longer than expected to metamorphose were larger than average. When we combine this positive relationship between "residual age" and metamorphic length with the negative relationship between length at 43 days and age at metamorphosis, the two effectively cancel each other out. This may explain why age and length at metamorphosis were not significantly correlated.

The predictability of metamorphic age by the body length that individuals have reached as early as 18 days into larval life, and the observation that metamorphic age becomes increasingly predictable as larvae grow, suggests that consistency must exist in the relative size rank among individuals. Strong autocorrelations in length were detected using rank correlations (Table 3.6). Size at 43 days of age did not correlate strongly with length at metamorphosis as mentioned in the previous analysis. Rank correlations of growth rates from 0-18 days versus that from 18-30 days ($r=0.11$-0.28) and growth over the 18-30 day period versus that for 30-43 days ($r=0.5$-0.7) suggest that the strong size autocorrelations are only partly due to autocorrelation in growth rate (i.e. fast growers being more likely to grow quickly at later times). Therefore early growth (and the size achieved) may be important in determining how larvae rank in length relative to one another at later times.

Discussion

Growth rate proved to be important in determining the timing (age and size) of metamorphosis both among and within populations of yellowtail flounder, consistent with my synthesis of existing data on other species (Chapter 2). Although temperature may determine the growth potential of larvae, affecting the location or mean of the distribution of metamorphic ages and sizes (Figure 3.1), the considerable dispersion about the mean suggests that individual characters vary in a continuous manner. If this is the case, then averaging the metamorphic traits of individuals in comparisons of different rearing environments (e.g. Crawford 1984; Seikai et al. 1986; Minami and Tanaka 1992) may mask individual level responses that vary continuously with individual growth trajectories. Below, I summarize evidence that this may be true.

Because individual average growth rates ($mm \cdot day^{-1}$) are not independent of either age or length at metamorphosis, any hypothesis testing and estimates of explained variance are inappropriate, however, the slopes and intercepts of the relationships are nonetheless valid estimates (D. Schneider, Memorial University of Newfoundland, *pers. comm.*). Consequently the relationships between growth and age or length at metamorphosis can be compared across environments. In my study, increasing growth rates decreased the age at which individuals underwent metamorphosis (Figure 3.7), and the relationship was continuous across temperatures and tanks suggesting that growth rate averaged over the entire larval stage roughly determines individual ages at metamorphosis. The effect of growth rate in determining individual lengths at metamorphosis is not as simple. Overall length at metamorphosis

increases with growth rate as does the range of lengths for a given growth rate. As growth increases, the increasing range of lengths might suggest a dependence of individual lengths on the growth rate experienced by larvae later during ontogeny, once age at metamorphosis has been roughly established (as in the otolith study). For a given time interval prior to metamorphosis, a 10% change in growth rate will have a greater absolute impact on final size for larvae that were growing rapidly, resulting in a greater range of lengths.

Data from the otolith reconstructions further suggest that although average growth rates may roughly determine age and length at metamorphosis, precise predictions of the timing require examination of the variability in daily growth experienced by individuals over the course of their larval life. Although strong autocorrelations were detected in the sizes of larvae over time, this was only partly due to autocorrelation in growth rates. Such size autocorrelations have also been found in larval red sea bream (Umino et al. 1996), juvenile turbot, *Scophthalmus maximus* (Rosenberg and Haugen 1982; Imsland et al. 1996) and halibut, *Hippoglossus hippoglossus* (Hallaråker et al. 1995). Likewise, Chambers and Miller (1995) found similar degrees of autocorrelation in larval Atlantic menhaden (*Brevoortia tyrannus*) for similar time spans between measurements (10-15 days) and also found that growth autocorrelations were weaker than those for size. The weaker rank correlations for growth rate suggest that the growth rate and the absolute size achieved early during larval life may be important in determining the timing of metamorphosis. Individual growth curves for winter flounder (*Pleuronectes americanus*) larvae from hatch to the

completion of metamorphosis appear sigmoidal (Bertram et al. 1997), a consequence of proportional growth in length early on, and a lack of growth during metamorphosis (Rosenberg and Laroche 1982). As a result, the first half of larval life (particularly once feeding is initiated) may be a period in which body length increases almost exponentially, creating the potential for the establishment of difference among individuals that may persist well into the larval period.

In addition to the importance of growth rates during early ontogeny, data from the otolith diameters also suggest that the precise timing of metamorphosis depends on the growth experienced in the latter half of larval life. Individuals that underwent metamorphosis sooner than would be predicted by their growth rate up to day 43 did so at a smaller size (the opposite being true for individuals that took longer than predicted). Unfortunately I do not have an estimate of growth rate from 43 days to metamorphosis that is independent of metamorphic length, precluding me from finding what determines whether an individual will metamorphose sooner/smaller or later/larger than predicted. In addition to the results from the otolith study, the density-dependent effects observed in some of the tanks at 11°C may support the argument that growth later in larval life affects the timing of metamorphosis. A potential mechanism for the development of a positive correlation between age and length is that as densities in the aquaria decreased due to the removal of metamorphosed individuals, the remaining individuals experienced a decrease in competition as food was partitioned among fewer larvae (i.e., increased growth rate). The results of the otolith study suggest that these remaining individuals are the slower

growing members of the population (developmentally further from metamorphosis), and thus have a longer time to utilize these benefits and grow to larger sizes. This may explain why some of the largest fish at 11°C were from the higher density tanks.

Although the density-dependent effects observed at 11°C were the result of survival variability, and not intentionally included in the experiment, their occurrence has allowed me to explicitly quantify any laboratory artifacts present in my study. Although such strong density effects are unlikely in more natural situations (e.g. Fortier and Harris 1989), by quantifying the effects I am able to predict the ages and sizes at metamorphosis expected in the wild. Results from the less dense populations and from the biphasic regression analysis suggest that age and length at metamorphosis are not expected to be strongly correlated under growth rates similar to those in this study, and more natural fish densities. This result conforms with those presented in Chapter 2, where I found that the correlation between individual metamorphic ages and lengths improves as mean growth rate increases, but correlations become strong and positive only beyond growth rates of about 0.40 $mm \cdot day^{-1}$. Considering the individual responses of age and length, we would predict that the distribution of age at metamorphosis would be positively skewed in the wild for larvae with similar growth rates as those involved in this study. Such a result was predicted in Chapter 2, where I argued that metamorphic age should be lognormally distributed. Extrapolating my results towards the lower densities expected in more natural situations, we would predict that length at metamorphosis be more or less distributed normally, with a symmetric distribution.

The greatest source of error in this study is that associated with inferring ranks in body length from otolith diameters for groups of same-age larvae (i.e. using diameter as a relative index of length). This error is most true for the fish at 18 days of age. At such a young age (and small size), when the range of sizes within the population is small, the variance explained by the relationship between length and otolith diameter is less than at larger average sizes. This effect is partly due to measurement error, as I was limited to an accuracy of ±0.5 μm at a magnification of 1000x, which may be significant given that measured otolith diameters at 18 days ranged only from 21-33.5 μm. In addition there was appreciable error between measurements made on left versus right lapilli at this age. Considered jointly, these sources of error may have weakened the relationship between back-calculated length at 18 days and age at metamorphosis. These sources of error would have been substantially less important for 30 day old larvae as the fish length/otolith diameter relationship was tighter and right and left otoliths became more similar. Umino et al. (1996) also found that the relationship relating otolith diameter and body length improved dramatically as fish grew from first feeding, where the two variables were initially uncorrelated.

The results of this study of individual variability in the timing of metamorphosis, suggest that transition age and length are determined by variation in the growth rate of larvae occurring throughout early development. We begin to see the generation of variability in metamorphic traits early during ontogeny, and consequently events early on can set the stage for the rest of larval life. This is exemplified by the

relationship between age at metamorphosis and the size of larvae at 18 days. In addition to the importance of events during early ontogeny, our results suggest that variability in growth rate right up to metamorphosis may determine the precise age, and particularly the length, at metamorphosis. Overall, these cumulative growth effects may be important in determining which individuals survive past metamorphosis, and ultimately in determining recruitment variability, as meta-analyses suggest that recruitment begins to be established around that time (Bradford 1992, Bradford and Cabana 1997). Given that metamorphic age represents the duration of the larval period (a time of high rates of mortality), and that individual metamorphic ages become roughly established early during ontogeny, the cumulative probability that an individual will survive to metamorphosis may also become established soon after hatching. The results of this study and others (Chambers et al. 1988, 1989, Bell et al. 1995, Benoît et al. 1999 *in review*) suggest that the variability among individuals in the age-at-size, size-at-age and timing of early life history transitions, along with the dependence of this variability on environmental (growth) factors, creates the potential for substantial recruitment variability under very simple assumptions regarding mortality rates (Bell 1997).

Table 3.1 Number of larvae surviving to metamorphosis (n) and larvae that were removed from the experiment prior to metamorphosis (c) in each tank, along with the mean ages and lengths at metamorphosis (+/- SD), and Kendall's tau (τ) nonparametric correlation between age and length. All values of τ were statistically significant ($P<0.05$) except where indicated (ns). Tanks in which otoliths were stained are denoted by an asterisk.

temp.	tank	n	c	mean age (days)	SD	mean length (mm)	SD	Kendall's τ
7°C	1	25	2	118.0	14.5	17.1	2.3	-0.41
	2	84		118.0	10.7	17.2	2.0	0.24
	3	17	1	121.0	10.6	15.8	1.7	-0.09 ns
	4	13		121.8	16.0	15.3	2.4	-0.58
	5	4	1	110.0	8.7	16.2	1.5	-0.91 ns
11°C	1	195		111.9	16.6	16.9	2.3	0.52
	2*	62		81.2	9.5	18.0	2.2	0.23
	3	161		97.5	15.7	16.4	2.0	0.32
	4*	104		86.6	12.0	18.0	2.1	0.21
	5	36		86.0	15.0	19.0	2.8	-0.28 ns
	6	167		93.8	13.8	17.0	2.3	0.41
	7*	41		75.1	10.2	19.7	3.2	0.16 ns
13°C	1	71		75.4	11.9	18.9	2.2	-0.05 ns

Table 3.2 Results of segmented regression analyses on individual measures of age and length at metamorphosis for those tanks that display a biphasic relationship. Parameter estimates are given with lower and upper confidence intervals. See text for details regarding the analyses.

Temp.	Tank	d.f.	R^2 (corrected)	Intercept	Slope 1	Slope 2	Break
11°C	1	4, 191	0.53	22.4 (17.3, 27.5)	-0.08 (-0.14, -0.03)	0.24 (0.17, 0.30)	97.9 (93.6, 102.1)
	3	4, 157	0.41	19.2 (16.3, 22.2)	-0.05 (-0.08, -0.01)	0.21 (0.16, 0.27)	95.9 (91.9-99.9)
	4	4, 100	0.29	18.6 (14.7, 22.5)	-0.02 (-0.06. 0.03)	0.22 (0.12, 0.31)	89.0 (87.9, 90.1)
	6	4, 163	0.45	13.6 (10.1, 17.1)	0.03 (-0.01, 0.07)	0.17 (0.09, 0.24)	96.2 (90.3, 102.1)

Table 3.3 Fit to the accelerated failure model (equation 4) for log-transformed metamorphic ages and lengths.

		Age at metamorphosis				**Length at metamorphosis**			
	d.f.	Estimate	SE	χ^2	P	Estimate	SE	χ^2	P
Intercept	1	4.27	0.02	57039.9	<0.0001	3.04	0.02	28619.2	<0.0001
Temperatu 7	1	0.460	0.021	498.0	<0.0001	-0.116	0.021	32.0	<0.0001
11	1	0.101	0.026	29.6	<0.0001	-0.013	0.019	0.50	0.48
13	1	0	0	-	-	0	0		-
Density	1	1.78×10^{-3}	0.90×10^{-3}	416.0	<0.0001	-0.83×10^{-3}	0.90×10^{-5}	86.2	<0.0001
Scale	1	0.140	0.003			0.141	0.003		
log-likelihood:		441.1				503.5			

Table 3.4.Temperature-specific fit of the accelerated failure model (equation 4) to log-transformed metamorphic lengths, including the effects of age and density.

	Parameter estimate	SE	Chi-sq.	P
7°C				
Intercept	2.67	0.11	602	<0.0001
Age ($x10^{-3}$)	1.50	0.98	2.36	>0.1
Density ($x10^{-3}$)	0.61	0.327	3.48	0.062
Scale	0.11	0.007		
11°C				
Intercept	2.74	0.02	18071	<0.0001
Age ($x10^{-3}$)	4.55	0.23	386	<0.0001
Density ($x10^{-3}$)	-1.97	0.09	457	<0.0001
Scale	0.12	0.003		
13°C				
Intercept	2.75	0.085	1036	<0.0001
Age ($x10^{-3}$)	3.26	1.13	8.29	<0.005
Scale	0.11	0.010		

Table 3.5 Regressions relating otolith diameter and standard length for common aged larvae and larvae at metamorphosis, and regressions comparing the diameters of left and right otoliths at each staining period and at metamorphosis.

Regressions for back-calculation of length (SL = intercept+slope* otolith diameter)

	N	mean length (mm)	range (mm)	R^2	intercept (SE)	slope (SE)
11 day old [1]	28	4.49	4.02 - 5.07	0.77	2.08 (0.26)	0.10 (0.01)
20 day old [1]	40	7.04	4.99 - 9.17	0.84	-0.64 (0.54)	0.23 (0.02)
43 day old (stained)	30	10.07	6.92 - 14.6	0.93	2.74 (0.40)	0.13 (0.01)
At metamorphosis	186	18.22	12.9 - 32.4	0.59	3.20 (0.93)	0.10 (0.01)

Comparison of right and left otoliths (right diam.=intercept + slope*left diam.)

	N	mean diameter (mm)	range (mm)	R^2	intercept (SE)	slope (SE)
18 day old (stained)	117	28.31	21.0 - 33.5	0.64	8.03 (1.45)	0.72 (0.05)
30 day old (stained)	117	37.06	28.0 - 45.5	0.84	4.23 (1.39)	0.89 (0.04)
43 day old (stained)	117	54.85	36.0 - 89.0	0.97	1.39 (0.93)	0.98 (0.02)
At metamorphosis	117	146.82	104 - 230	0.91	3.31 (4.09)	0.97 (0.03)

[1] Measures were not made on larvae reared in the metamorphosis experiment. Larvae were taken from separate rearing stocks.

Table 3.6 Spearman rank correlations (and their statistical significance) for measurements made on otoliths stained with alizarin complexone. Age is the observed age at metamorphosis, length (Lx) is the diameter of the otolith at age 'x' or at metamorphosis (LM), and Δa,b is the growth rate from time 'a' to time 'b'.

Tank	n	Age-L18	Age-L30	Age-L43	Age-LM	Age(residual)-LM
2	50	-0.39**	-0.54***	-0.62***	0.16 ns	0.37**
4	97	-0.51***	-0.6***	-0.75***	0.2*	0.51***
7	39	-0.58***	-0.59***	-0.74***	0.22 ns	0.22 ns
7 [1]	38	-0.62***	-0.72***	-0.86***	0.14 ns	0.16 ns
all	186	-0.41***	-0.55***	-0.63***	0.08 ns	0.41***

		Length autocorrelation:			**Growth rate autocorrelation:**		
Tank	n	L18-L30	L30-L43	L43-LM	Δ0,18-Δ18,30	Δ18,30-Δ30,43	Δ30,43-Δ43,meta.
2	50	0.75***	0.89***	0.12 ns	0.11 ns	0.63***	0.34**
4	97	0.88***	0.91***	0.12 ns	0.28**	0.54***	0.20*
7	39	0.75***	0.92***	-0.03 ns	0.17 ns	0.7***	0.4*
7 [1]	38	0.84***	0.91***	-0.12 ns	0.21 ns	0.68***	0.36*
all	186	0.81***	0.91***	0.19*	0.21**	0.59***	0.16*

[1] strong outlier (length=32.4 mm) removed

ns P>0.05, * 0.01<P<0.05, ** 0.001<P<0.01, *** P<0.001

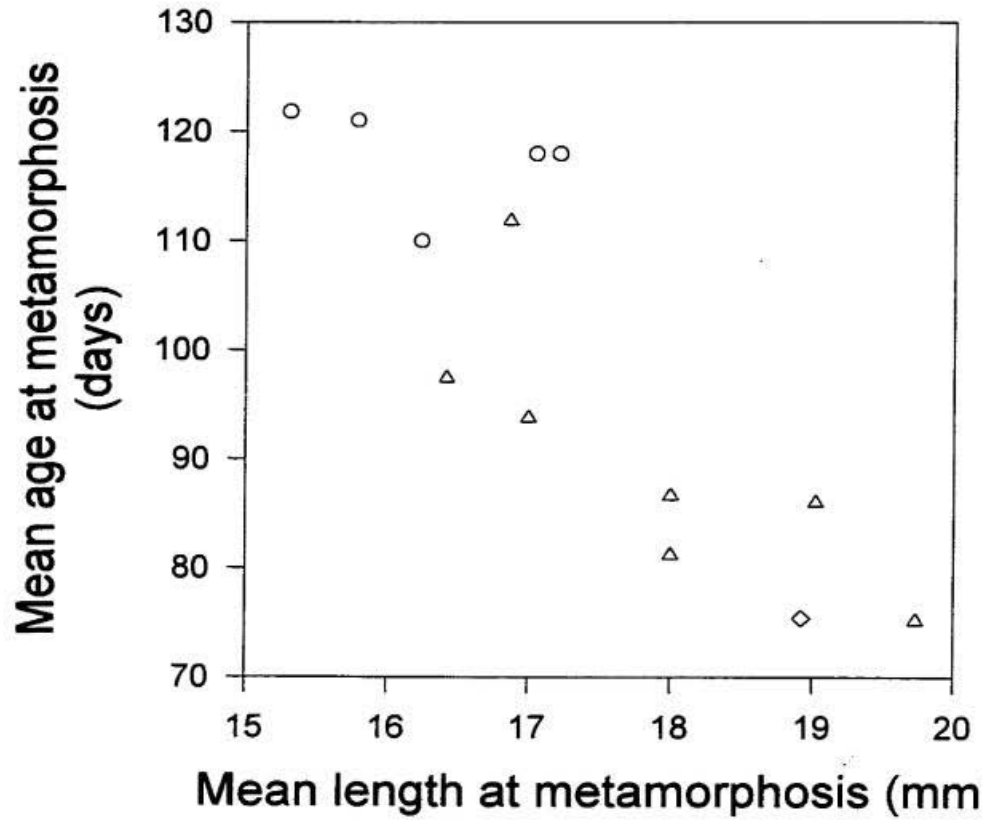


Figure 3.1 Relationship between mean age and length at metamorphosis in individual aquaria (temperature and replicate) (7°C (o), 11 °C (Δ) and 13 °C (◇)).

Figure 3.2 Ages and lengths at metamorphosis for each aquarium of laboratory-reared yellowtail flounder. Each point in the bivariate plots represents the response of one individual (see Table 3.1 for sample sizes). Frequency distributions are for the univariate responses of age and length. The scales for the distributions can be found on the secondary x and y-axes for age and length respectively. Note that tanks 4 & 5 from the 7°C treatment are combined in a single panel, with additive frequency bars.

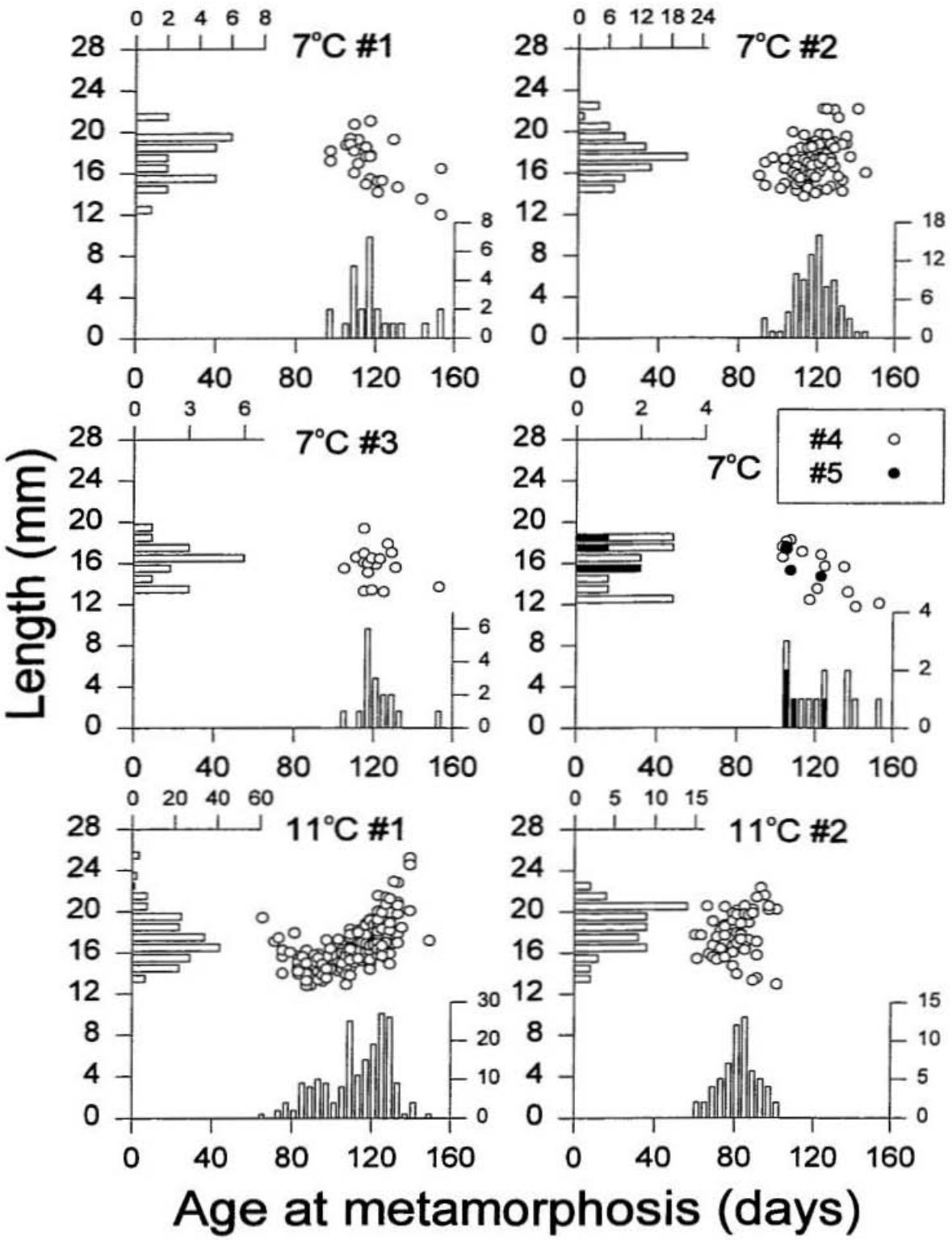
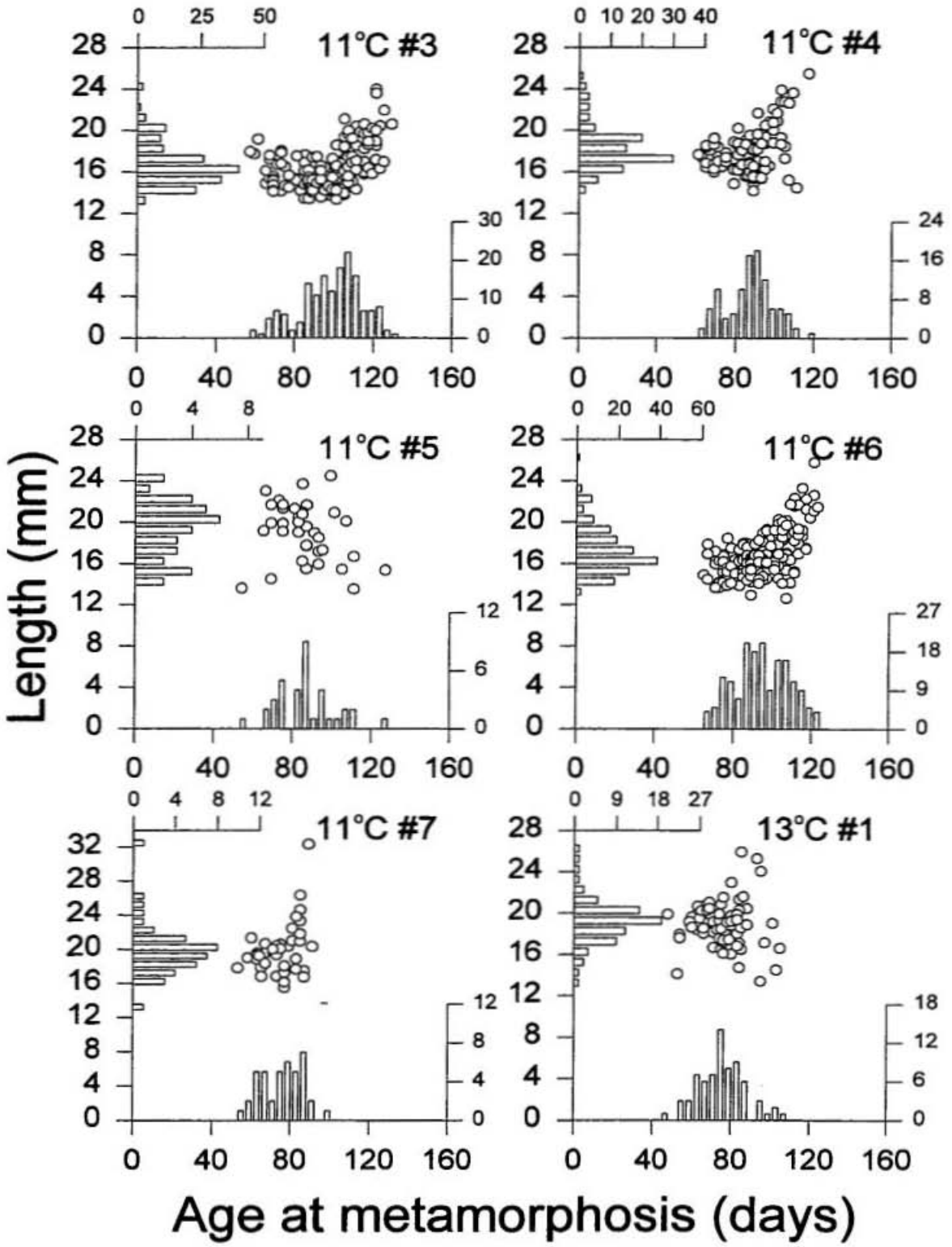

7°C #1
7°C #2
7°C #3
7°C
11°C #1
11°C #2
#4
#5
Length (mm)
Age at metamorphosis (days)

Figure 3.2, continued.


11°C #3
11°C #4
11°C #5
11°C #6
11°C #7
13°C #1
Length (mm)
Age at metamorphosis (days)

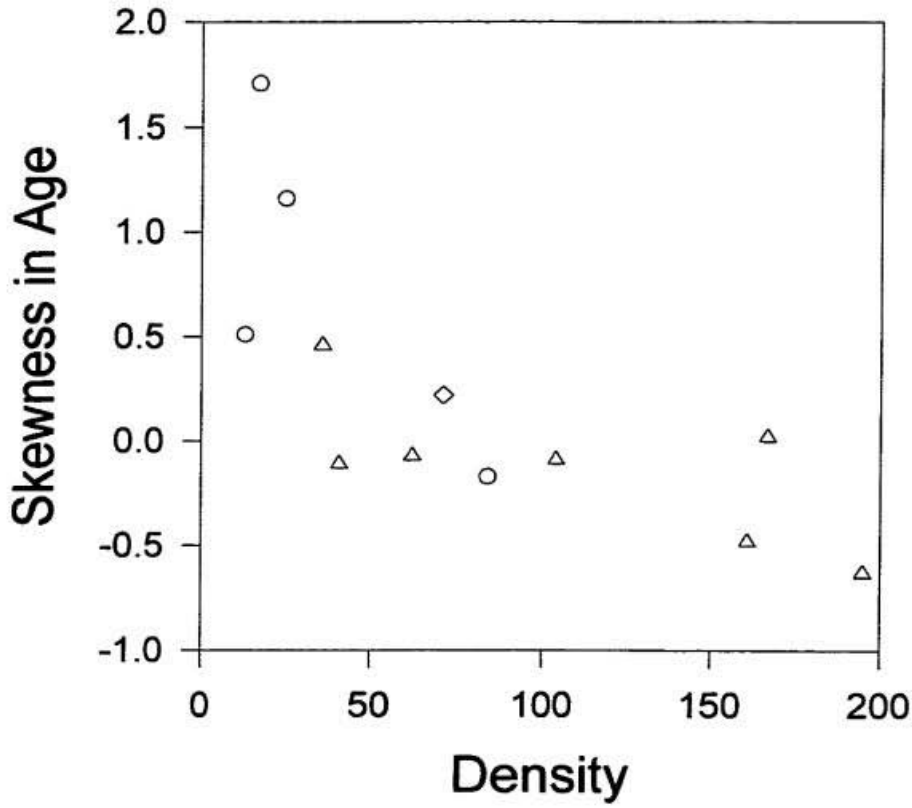


Figure 3.3 Effect of fish density on the skewness of the metamorphic age distribution in each tank (7°C (o), 11 °C (Δ) and 13 °C (◇)).

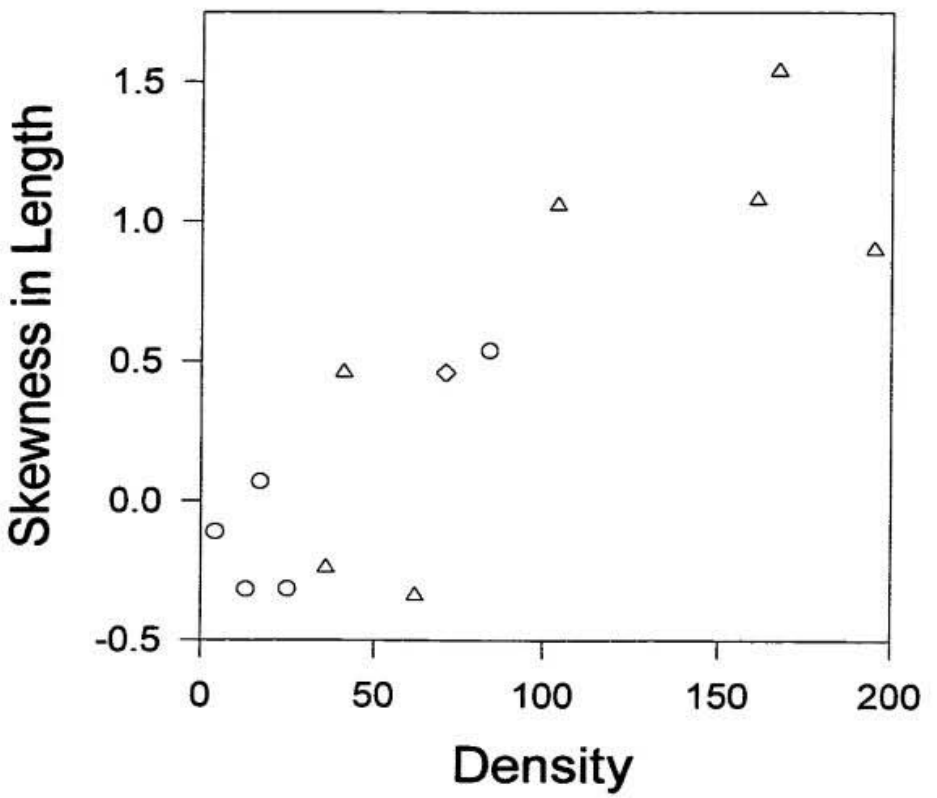


Figure 3.4 Effect of fish density on the skewness of the metamorphic length distribution in each tank (7°C (o), 11 °C (Δ) and 13 °C (◇)).

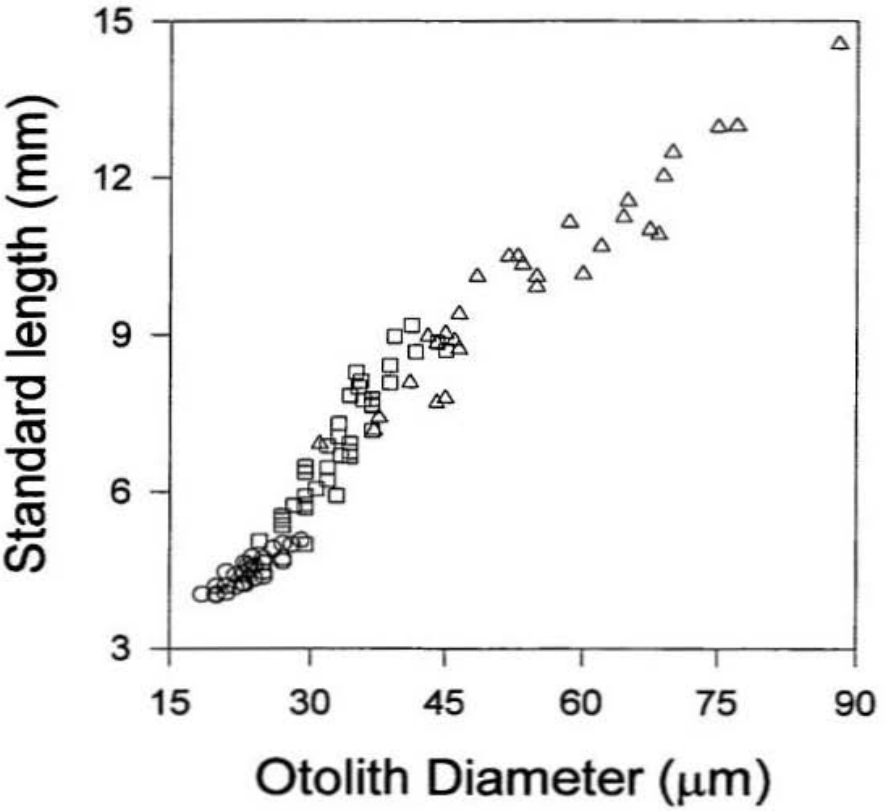


Figure 3.5 Relationship between otolith diameter and standard body length for larvae from different age classes (11 day old larvae (o), 20 day old (□), and 43 day old (Δ)).

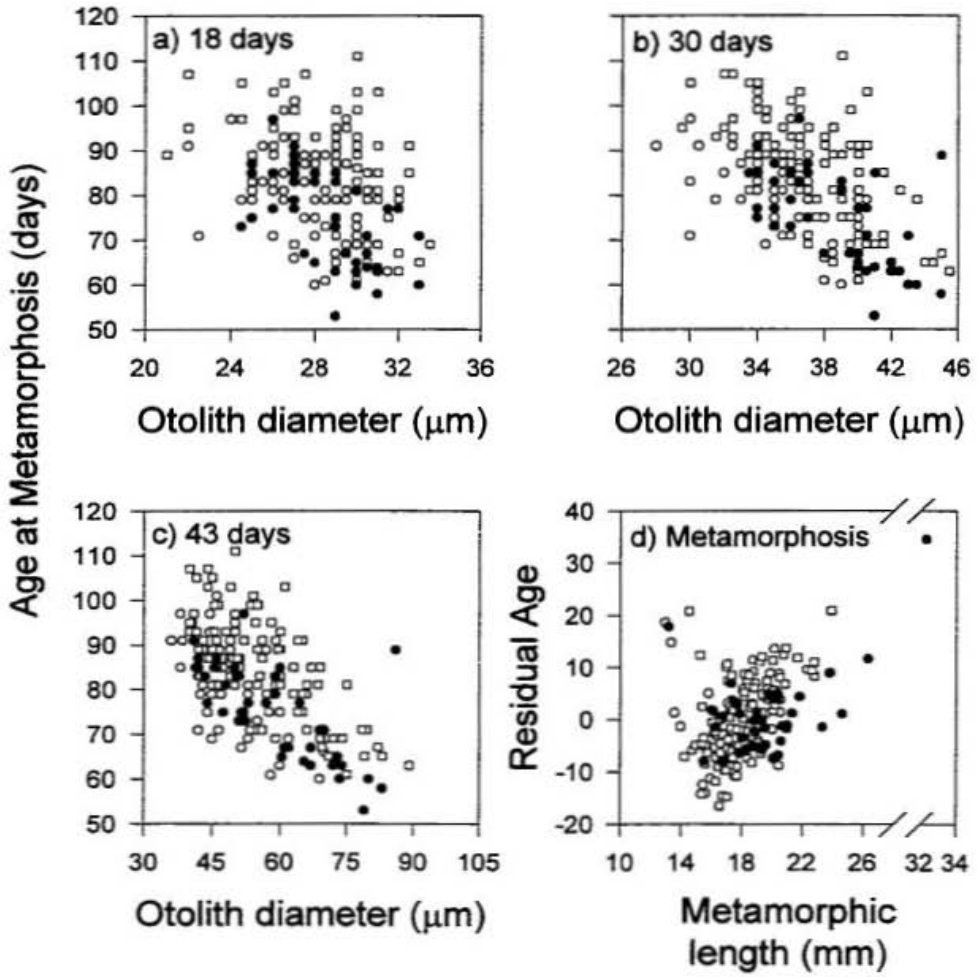


Figure 3.6 Relationship between age at metamorphosis and otolith diameter at (a) 18 days, (b) 30 days, and (c) 43 days of age, for tanks 2 (o), 4 (□) and 7 (●), at 11°C. Panel (d) is the relationship between the residuals from panel (c) and length at metamorphosis. Residuals were calculated from regressions relating otolith diameter at 43 days and age at metamorphosis for each tank.

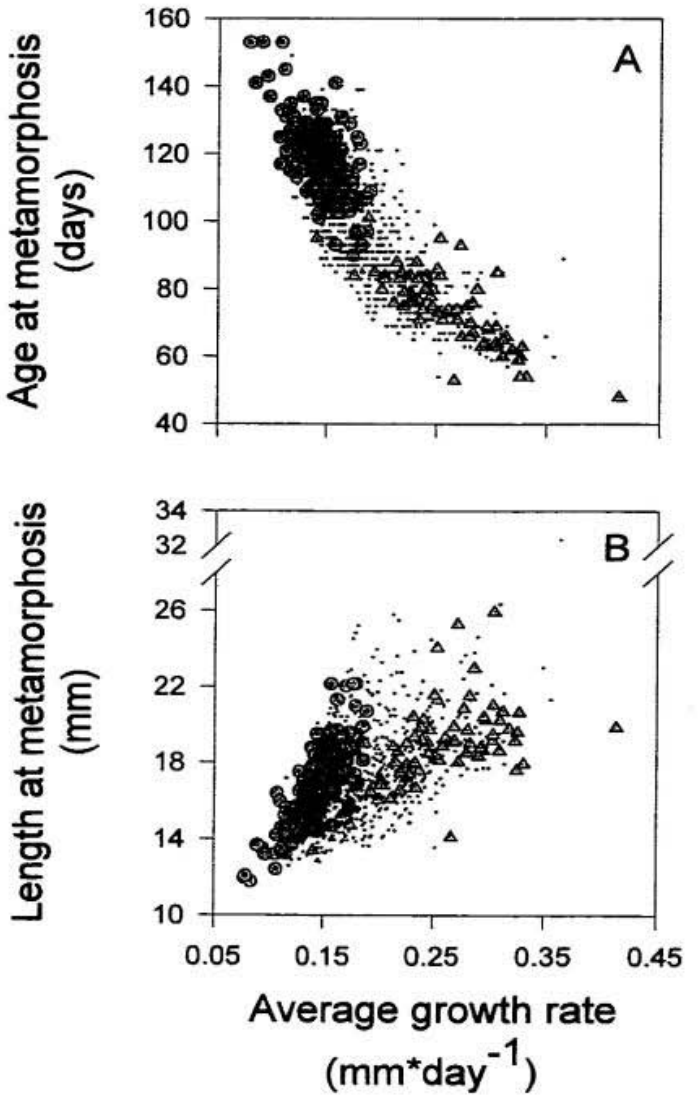


Figure 3.7 Relationship between the growth rate of individual larvae, averaged over the entire larval period, and (a) age, or (b) length at metamorphosis (7 (•), 11(.), and 13 °C (▲)).

Chapter 4

The interaction of rearing temperature and maternal influence on egg development rates and larval size at hatch in Yellowtail flounder (*Pleuronectes ferrugineus*)

Abstract

I assessed the extent to which temperature interacts with maternal contributions to egg size to affect development time and size of yellowtail flounder (*Pleuronectes ferrugineus*) larvae at hatching. Maternal effects contributed significantly to differences in egg sizes produced by four females. Eggs from each female were incubated at five temperatures. Development time was most significantly affected by temperature, and female effects were minimal. However, the variance in development time within a population was significantly affected by an interaction between female and temperature effects. Average length at hatch varied significantly among temperatures and females, as did the variance in hatching length within a population. Variance in hatching length explained by maternal effects peaked at intermediate temperatures (~38% explained variance at 7°C), while variance explained by covariation with development time increased linearly with temperature, explaining ~40% variance at 13°C. Overall, the non-additive interaction between maternal contributions and the environment suggest that female effects must be considered over the entire range of environmental conditions experienced by their progeny. In addition, my results support the idea that it is inappropriate to quantify female effects among eggs and extrapolate these differences to larvae.

Introduction

The timing of early life history transitions (i.e. hatch, first feeding, metamorphosis) in fishes has the potential to influence survival and recruitment, as these transitions often involve niche shifts whereby young fishes may encounter different sources of mortality. Variation in the timing may be critical during a period where mortality rates are large and variable (Pepin 1991; Bradford 1992). In addition to variation in the age and size of early life history transitions among species (Miller et al. 1988; Duarte and Alcaraz 1989; Pepin 1991), there is often considerable variability among populations of the same species (Pauly and Pullin 1988; Chapter 2), and among individuals within a single population (Chambers et al. 1989; Pepin et al. 1997; Chapter 2). Consideration of this variability is important because selective mortality, if present, occurs at the individual level (Sharp 1987; Rice et al. 1993). Although theoretical and empirical considerations have shown that small changes in the average growth and mortality rates of a cohort can have large consequences to recruitment variability (Beyer 1989; Bell et al. 1995), the dispersion and distribution of sizes and ages at transition points (and consequently individual growth rates) may be of equal or greater importance (Pepin 1989; Rice et al. 1993).

Variation in early life history traits among individuals (within a population), under relatively homogeneous environmental conditions (salinity, temperature, etc.), can be partitioned into two broad categories: differences due to parentage (usually maternal) and among-sibling differences (Chambers and Leggett 1989a, 1992, 1996; Chambers et. al. 1989). Females of the same species, differing in age, size, condition,

or timing of spawning within the reproductive season (for batch spawners), will produce eggs of different sizes, possessing different quantities of yolk (reviewed in Chambers and Leggett 1996; Trippel et al. 1997). There is evidence that these female effects can further translate beyond hatching, resulting in variation in size and growth rates of larvae within a population (Knutsen and Tilseth 1985; Chambers et al. 1989; Chambers and Leggett 1989a,b; Buckley et al. 1991). Quantification of the maternal origins of within-population variation in size, condition and growth rates of larvae, beyond simple correlation or comparison studies, has been limited. Given the difficulties in rearing marine fish larvae, variation in egg size is often quantified, and then inappropriately extrapolated to larvae using species level correlations (Pepin and Miller 1993; briefly reviewed by Chambers and Leggett 1996). The alternative approach has been to compare mean egg diameters and average larval size of batches of sibling eggs, among females (e.g. Knutsen and Tilseth 1985; Marteinsdottir and Steinarsson 1996). By considering only average responses, this approach ignores the variability of sizes among siblings within a batch, and overemphasizes maternal contributions (i.e. although mean size may differ among females, the distributions of sizes may overlap substantially).

Past studies of maternal influence (with the exception of Chambers et al. 1989) have not considered an important aspect of embryonic development, namely the development time from fertilization to hatch. Maternal effects may be important as cross-species analyses have shown that development time may be related in part to egg size (Pauly and Pullin 1988; Duarte and Alcaraz 1989; Pepin 1991). In addition, there

are no studies to my knowledge for marine fishes (Bengston et al. 1987 is the closest exception) that have thoroughly quantified the possible interaction between female and environmental factors (such as the dominant effect of temperature on development times (Pauly and Pullin 1988; Duarte and Alcaraz 1989; Pepin 1991)). There is a substantial basis for investigating this issue given that many species show a change in length at hatch with increasing temperature (reviewed in Chambers 1997). Consequently, because both development time and size vary with temperature, the power to detect maternal effects and the proportion of the variance that can be explained by maternal influence may also change with temperature.

In this chapter I examine the relationship between maternal contributions and rearing temperature in determining variability in the hatching characteristics of yellowtail flounder (*Pleuronectes ferrugineus*) eggs. Specifically, I quantify the amount of variance in egg sizes that can be attributed to female differences, and determine the extent to which these maternal effects are important in determining variability in length at hatch and development time of the embryos. I consider the effects of temperature and maternity on the entire distribution of hatching larvae (mean and variance). The motivation for this study comes largely from the observation in the previous chapter that initial differences in body size and growth rate, occurring around or soon after hatching, can persist well into the larval period, to affect the timing of metamorphosis. Consequently it is important to understand the factors which cause this initial variability.

Methods and Materials

Species Studied- Relevant information

Yellowtail flounder are iteroparous batch spawners, producing several batches of pelagic eggs per season. As with other batch spawners (e.g. cod, *Gadus morhua*), egg size can vary among seasons, among females within a season, among batches within females and within batches (A. J. Manning, Ocean Sciences Center, Memorial University of Newfoundland, personal communication; Chambers and Waiwood 1996). In addition, hatching size of larvae has been found to vary with rearing temperatures (Laurence and Huntting Howell 1981).

Experimental Design

I used a two-way factorial design to examine the effects of maternal influence (4 females), rearing temperature (5 temperatures) and their possible interaction on developmental rate and length at hatch of yellowtail flounder eggs. Five 225-L water baths were maintained at approximately 5.5, 7, 9, 11, and 13 °C (Table 4.1 for realized temperatures). Twelve 250-mL glass jars filled with filtered and UV sterilized sea water were placed in each water bath and used as static rearing containers for the eggs. Three replicate jars of eggs from each female were reared at each of the five temperatures. A 17 hour light, 7 hour dark photoperiod, representative of the natural photoperiod experienced during yellowtail flounder spawning in the wild, was maintained by

fluorescent lights hung approximately one meter above the tanks. Temperatures were measured three times daily (at approximately 9:00, 13:00, 17:00) using a digital thermometer, with 0.1 °C accuracy. In general, temperatures varied little both in terms of variance and range within each water bath (Table 4.1). As well, the individual time series of temperatures were deemed stationary (no long term trends or cycles) by visual inspection.

Yellowtail flounder eggs were obtained by manual stripping on two consecutive mornings (eggs from two females were collected on each day) from a broodstock held for 2-3 years at the Ocean Sciences Center, Memorial University of Newfoundland (Canada) (Table 4.2). An aliquot of 0.5 mL of eggs (yielding ~1143 ± 42 eggs) from each female was placed into each of fifteen 20-mL plastic vials that were then allowed to acclimate to the rearing temperature for 20 minutes prior to fertilization. After acclimation, 0.2 mL of mixed sperm from three separate males (same males for both days), was added to all the plastic vials and the mixtures were gently swirled to ensure mixing of gametes. Filtered sea water (5 mL) was then added to each vial in order to activate the sperm. Fertilization was allowed to take place for two minutes before the fertilized eggs were gently poured into the glass rearing jars. Immediately following the fertilizations, surplus eggs from each female were measured under 250 times magnification using a digital imaging system (Bioscan OPTIMAS® 4.10) to obtain a size distribution of egg diameters for each female.

One half of the water in the rearing jars was replaced with filtered/sterilized water every three days by siphoning from the bottom to remove dead eggs. At the first

water change, 100 mg•L^{-1} of Streptomycin and 60 mg•L^{-1} of Penicillin were added to the containers.

Once hatching had begun, rearing containers were checked for newly hatched larvae every two hours (24 hours per day) in the 13, 11 and 9 °C treatments and every four hours at 7 and 5.5 °C. The coarser sampling interval at the lower temperatures did not jeopardize estimates of mean and variance of hatching time as the hatching period at these temperatures is more protracted than in the other treatments. All newly hatched larvae were collected using a modified plastic pipette, and immediately preserved in 4% formalin. Over the course of the experiment, approximately 10 larvae were collected from each temperature/female treatment and measured live for standard length (from the tip of the snout to the end of the notochord), as well as yolk sac length and diameter, before being preserved in individual containers (see measurement protocol below). This resulted in 209 larvae that were subsequently re-measured six weeks later (when all hatching larvae were measured) to quantify the effects of the preservation on body dimensions.

All of the preserved larvae were measured for standard length under 250x magnification using the imaging system. Yolk sac dimensions (length and depth) were also measured. Some larvae were damaged during collection with the pipette (<9%) and highly accurate measurements could not be made. Consequently, these larvae were only used in the analysis for development time, resulting in larger sample sizes as compared to those for hatch length. Development time was quantified in hours from fertilization to hatch.

Analysis

General linear modelling (GLM) techniques were used in my analysis as they can incorporate any combination of categorical, ratio and nested explanatory variables. In addition, they are robust to unequal sample sizes.

Individual measurements of egg diameter were partitioned into female and error (within-female) effects for hypothesis testing. Replicate rearing containers were used as the units of study for the analyses of hatching length (HL) and development time (DT) (i.e. average HL and DT per replicate) in a two-way random-effects ANOVA, with females and temperatures as independent variables. Given that sample size differed among the treatments and replicates, each replicate was weighted by the sample size that went into calculating the mean HL or DT. The coefficients of variation (CV) for HL and DT (per replicate) were each considered in a weighted random-effects GLM similar to that used for the average response.

As several studies have found covariation between DT and HL at the level of the individual (e.g. Alderdice and Velsen 1971; Alderdice and Forrester 1974), I related the HL of individual larvae to DT, female effects, and replicates (nested within female effects) in an analysis of covariance. Analyses were performed for each temperature treatment to facilitate interpretation of the results, given that the mean and variance in HL could both be affected by temperature and maternal effects. I examined the residuals for all of the analyses, and transformed the response variables where appropriate to meet the assumptions of the tests.

To examine the biological relevance of the effects used to explain variation in egg diameter, HL and DT, I estimated variance components for the explanatory variables (Chambers and Leggett 1989a). Such an analysis is important because statistical significance of an explanatory variable is not always indicative of its biological (variance-generating) importance. Variance components were estimated using log-likelihood techniques by equating the mean square (MS) or variance of each effect in the linear model to an expected MS. Expected MS depend on the structure of the model (whether it is a fixed, random or mixed-effects model), the number of levels for each effect, sample sizes, as well as the relationship of the main effects (e.g. nested effects, interactions) (Sokal and Rohlf 1981). As this technique relies on creating an expected MS, and solving for each variance component, it can only be regarded as approximate (Sokal and Rohlf 1981). Although confidence intervals on estimated variance components can be created (Sokal and Rohlf 1981), that was not done given the relatively small number of female and temperature treatments used. Measurements on individual larvae were always used in the estimation of variance components, and consequently the error variance in the analyses represents the variation among larvae within replicates.

Results

Effects of preservation

Preservation in 4% formalin caused substantial shrinkage of the hatching larvae, with larger larvae being disproportionately affected (Figure 4.1). Preservation effects were estimated by fitting a negative exponential curve to the data of the form:

$$\text{preserved length} = \beta_o (1 - \exp(-\beta_1 \cdot \text{fresh length}))$$

where β_o is the asymptote of the curve, and β_1 determines the rate at which the asymptote is reached. This model was chosen over a linear model relating fresh and preserved lengths because it constrains the intercept of the curve to zero, although both models produced homogeneous and normally distributed residuals, and explained a similar proportion of the variance (66%). In general, the lack of correspondence for individuals was due to changing in the size rankings of individual larvae (Spearman-rank correlation coefficient of 0.79), rather than an absolute change in the variance of larval size after preservation (mean HL_{fresh} = 2.54 mm, coefficient of variation(CV) = 8.5%; mean $HL_{preserved}$ = 2.19, CV=8.6%). However, the distribution of preserved lengths was more leptokurtic (g_2=0.15) than that of fresh lengths (g_2=0.50). Analysis of variance using the residuals of the nonlinear fit showed that preservation effects did not differ among females ($F_{3, 199}$=1.08, P=0.36) or temperatures ($F_{4, 199}$=0.65, P=0.63).

Length and diameter of preserved yolk sacs were only measured when they were not damaged (>96% of the larvae). Although a significant relationship was found between fresh and preserved yolk sac lengths using the negative exponential model (β_0=1.45, asymptotic SE=0.19; β_1=0.89, ASE=0.18; P<0.0001), there was

comparatively little predictive power (R^2=0.40). Yolk sac diameter was affected to an even greater degree (β_0=0.64, ASE=0.04; β_1=2.86, ASE=0.45; R^2=0.14, P<0.0001) . As a result yolk sac dimensions were not included in my analyses.

Maternal effects

The females used in this experiment comprise a narrow range of lengths and weights for mature yellowtail flounder, minimizing the likelihood of a maternal effect that could be attributed to gross morphological differences. Nonetheless, egg diameter differed significantly among all 4 females as determined by analysis of variance ($F_{3, 355}$= 373.74, P<0.0001) with Tukey *a posteriori* multiple comparisons (Table 4.2, Figure 4.2). Female effects explained the largest proportion of the variance in egg diameters (82.5%), with the remaining variance being explained by variation in egg diameters within each batch of eggs (17.5%). The percent differences between the smallest and largest mean egg diameters (~13%), and smallest/largest individual egg diameters (~27%) used in my experiment were similar to the values reported in Chambers and Leggett (1996) for studies on maternal effects in other species based on a larger number of females. I therefore consider that despite the relatively small number of females used in my experiment, the differences among females are large enough that a female effect, if present, should be detected.

Using the initial number of eggs per container (~1140) and correcting for the percentage of eggs produced by each female that were capable of being fertilized (i.e. spherical, translucent and floating unfertilized eggs) (Table 4.2), I calculated a hatch

rate for each replicate container. It is important to note that this hatch rate is the percentage of unfertilized-viable eggs that were subsequently fertilized, and produced live larvae, and consequently includes the eggs that were never fertilized as well as embryos that died during development. The hatching rate of eggs was quite variable among females, temperatures and within temperature/female treatments (Figure 4.3). Results of a 2-way ANOVA on arcsine-square root transformed values (to normalize and homogenize the residuals) indicate a significant interaction between the temperature and maternal effects ($F_{12, 40}$=2.51, P=0.015). Hatching rate of eggs from females A and D was relatively constant across temperatures, but much lower for female A (Figure 4.3). Eggs from females B had a relatively high rate at the three lowest temperatures, but lower at the other temperatures. The hatching rate was low at the three lowest temperatures for female C, and nil at 11° and 13 °C.

Mean development time (DT) showed a significant exponential response to temperature, but maternal effects did not significantly affect DT (Table 4.3, Figure 4.4). In the face of the strong influence of temperature on DT, the variance contributions of all other variables was very small (Table 4.3). The change in the coefficient of variation (CV) of DT (per replicate) across temperature treatments differed significantly among females (female*temperature interaction, P=0.0213) (Table 4.3, Figure 4.4). This effect explained about 35% of the variation in CVs of DT, leaving 12% to be explained by temperature effects, and the remainder (53%) by variation among replicates within treatments (Table 4.3).

Length at hatch (HL) varied considerably among temperatures and females (Figure 4.5), with the largest individual larva (2.68 mm) measuring twice the length of the smallest (1.33 mm), and smallest/largest mean lengths differing by 20%. The maternal effects on average HL were not independent of temperature (female*temperature interaction, P=0.0023) (Table 4.4, Figure 4.5). The majority of the variance in the length at hatch of individual larvae was explained by variation among larvae within replicates (65.5%), and by maternal effects (22%) (Table 4.4). The remaining variance was explained by temperature and female*temperature effects.

In general, the CV in HL was greatest at the lowest temperature and decreased with increasing temperature (Figure 4.5). The variability in HL within rearing containers differed significantly among females (P<0.0001) and rearing temperatures (P<0.0001), although the latter explained more of the variance (Table 4.4). The interaction between the effects was very close to my Type I error criterion of α=0.05 (Table 4.4), and consequently I take caution in viewing the female and temperature effects as acting in an additive manner. Female effects and their interaction with temperature explained about one third of the variance in the CV of HL, with a further third explained by temperature effects, and the remaining third by variation among replicates (Table 4.4).

Because of the overriding influence of temperature on DT, the significance and variance contributions of female, replicate and within-replicate effects were considered for each temperature treatment (Table 4.5). Maternal effects were statistically insignificant at each temperature, and explained a small proportion of the variance (0-

16%). The variance explained by female effects did not vary in any systematic way with temperature. Most of the variance in DT within temperature treatments was explained by variation among replicates (which had statistically significant effects on DT in all treatments), and by variation among individual larvae (37-66% of the variance in DT) (Table 4.5).

Given the significant interaction between maternal and temperature effects on HL, I considered the former within each temperature level. Maternal effects were highly significant at the lower temperatures, but were borderline significant at 13°C (Table 4.5). The variance explained by maternal effects peaked at 7°C (47%) and was lowest at 13°C (15%). Replicate effects were statistically significant at all temperatures, but they did not explain much of the variance in HL (1.6-7%). Difference in HL among larvae within replicates explained a large proportion of the variance (51-78%).

Using the same model as that used to analyze the average HL among containers, I incorporated the covariance effects of DT of individual larvae on HL in an analysis of covariance performed at each temperature. Because the analysis was performed using individuals as the unit of study (resulting in large error degrees of freedom, and greatly increasing the likelihood of committing a Type I error), all of the effects (DT, female, DT*female, and replicates) were highly significant (specific values are not given, but $P<0.0071$ for all effects, at all temperatures). Maternal effects show the parabolic pattern described above (Table 4.5), with explained variance peaking at 7°C (Figure 4.6). At the lowest temperature, maternal effects are manifested by difference in

DT:HL covariances among females (i.e. differences in slopes). The variance explained by the interaction term was close to half of the total variance at 5.5°C, but decreased sharply thereafter (Figure 4.6). The variance in HL explained solely by DT increased approximately linearly with temperature, and was over 40% at 13°C. Variance explained by replicate and among individual (within replicate) effects were relatively constant across temperatures, and averaged 3% and 40% respectively.

Given the variability in hatching rate among females, temperatures and within treatments (Figure 4.3), possibly resulting in biased estimates of maternally derived variance due to disproportionate representation of the females, I wanted to verify the robustness of the variance components estimated from the ANCOVA. Consequently I re-analyzed the data at each temperature by randomly selecting larvae from each female (regardless of the replicate) such that the number of larvae that each female contributed to the analysis was equal. Despite the substantial reduction in sample size at each temperature that this caused (59, 71, 76, 71, and 50% reduction from 5.5°C to 13°C), the general trends in the explained variance were consistent with the previous analysis (Figure 4.6). Notable differences are that variance explained by maternal effects was greatest at both 7 and 9°C, rather than a sharp peak, the DT*female interaction is small at all temperatures, and error variance was greater and was more variable across temperatures. The increase in error variance along with a slight decrease in the clarity of the trends across temperatures may be explained by the decreased sample size used, because the estimation of variance is highly dependent on sample size (Sokal and Rohlf 1981). Those considerations aside, this re-analysis demonstrates that the non-additive

effects of temperature and maternal effects are robust to differences in hatching success.

Discussion

Maternal effects significantly influence the length at hatch (HL) of yellowtail flounder larvae, but had inconsequential effects on the development time (DT) of the eggs, both across and within temperatures. Most interestingly, the maternal contributions to HL were non-additively influenced by rearing temperature. Overall, HL (averaged over all females) was greatest at intermediate temperatures. The response of eggs produced by the different females varied however, showing maximum larval lengths at different temperatures.

The most important aspect of my findings is the manner in which the factors affecting variation in HL change in their importance as temperature is increased (Figure 4.6). These results are consistent with observations from other taxa (mainly amphibians) in which the phenotypic consequences of different levels of maternal investments (e.g., egg size, yolk volume) vary with the environment experienced by the offspring (Hutchings 1991; Parichy and Kaplan 1995, and references cited therein; Bernardo 1996a,b). Despite errors associated with estimation of variance components, and the limited number of females used in my study, the patterns of explained variance for the various effects across temperatures are strong and consistent.

Maternal effects are greatest at the lowest temperatures, but the way in which they are manifested differs. At 5.5°C, maternal effects consist mainly of differences among females in the slope of the DT:HL covariation, whereas at 7°C, maternal effects are largely independent of DT. As temperature is increased, the importance of maternal effects diminishes, and development time alone explains an increasing proportion of the variance in HL. At 13°C over 80% of the variance in HL can be explained by the time from fertilization to hatch and by differences among siblings within a container. Interestingly, the average summer water temperatures experienced by eggs and larvae in the area where the broodstock was collected range from 5 to 14 °C (P. Pepin, Department of Fisheries and Oceans, St. John's, Newfoundland, unpublished data). The range of temperatures experienced by larvae means that the importance of maternal effects may vary substantially within a season, let alone among seasons or years. Furthermore, given the protracted batch-spawning season (repeat spawning within a season) of yellowtail flounder, the response of hatching size to temperature may differ depending on when the eggs are produced within the spawning season. This effect may be further pronounced given the common observation of decreased egg size over the spawning season in many batch producing spring/summer spawners (reviewed in Chambers 1997).

A further observation is that the variance components in HL explained by experimental error (replicate variance) and by differences among individuals within a population are relatively constant across temperatures. The consistent experimental error among temperatures increases the power of the conclusions reached regarding

variation in HL. The lack of any trend in the residual variance across temperatures suggests that I may have captured the dominant temperature-dependent factors that affect the variance of HL among sibling larvae. Of the average 40% of the variation in HL that was explained by variation among larvae within containers (error variance), it is possible that a substantial portion of the variability was due to preservation effects. This explanation is plausible given that shrinkage due to preservation was not consistent among all larvae, causing larvae to shift in the size rankings and adding variability that was unexplained by fresh length (34%). Another factor that may have contributed to the unexplained variance in HL is a paternal effect. However, the influence of males on larval fitness is poorly studied relative to maternal effects (Trippel et al. 1997). Therefore I cannot evaluate the consequence of this effect except to note that paternity does not significantly affect metamorphosing larvae in another flatfish, *Pleuronectes americanus* (Chambers and Leggett 1992).

An obvious question that remains however, is how robust my results are given the few females used in this experiment. Clearly the power of my analysis would have been increased if eggs from more females had been used, but in the face of resource limitations (time and tank space) this would have meant using fewer temperature treatments. Variation in egg diameters for the four females used in this study was strongly influenced by maternal effects (>80% explained variance). This value compares favorably with results from similar studies on capelin, *Mallotus villosus* (71% explained variance), winter flounder, *Pleuronectes americanus* (46%), and captive cod, *Gadus morhua* (35%, with an additional 26% explained variance due to batches within-

females) (Chambers and Leggett 1996; Chambers and Waiwood 1996). It is noteworthy that such a pronounced maternal effect was found despite having used the eggs from females of similar size. Although the females differed in weight, this doesn't seem to have affected the egg size, as the ranking of eggs sizes doesn't match that of female weight or condition (judged as weight•length^{-3}). It is possible that egg size was affected by the age of the females (which is unknown as of yet) or their position in the spawning cycle (Chambers 1997). On the other side of the issue, one might argue that the limited number of females used may increase the likelihood of detecting a maternal effect, particularly if the results are driven by a single "aberrant" female. Visual inspection of Figure 4.5 suggests that this can't fully explain my results, as the reaction norms (the range of phenotypes expressed by a genotype across an environmental gradient) of each female differ from one another.

Once eggs are hatched and effects of temperature are included, the prominence of maternal effects is reduced substantially to an average of about 22% explained variance in larval size, with the majority of the variability residing among individuals within a container (~66%). The large decrease in the importance of maternal influence when going from egg size to hatching length is similar to that reported by Chambers et al. (1989) in capelin (71% variance in egg-yolk volume and 17% variance in HL due to females, although less disparate values are reported in Chambers and Leggett (1989a)). The persistence of maternal effects over time is an aspect that is poorly studied and underemphasized (see Bernardo 1996a for a review; Solemdal 1997). Maternal differences in egg size (within each of 2 age groups) disappeared 4 weeks after first

feeding in rainbow trout, *Salmo gairdineri* (Springate and Bromage 1985), and differences in initial egg size did not affect growth rates in larval and juvenile cod (Blom et al. 1994), or larval mummichog, *Fundulus heteroclitus* (Marteinsdottir and Able 1992). Interestingly, the maternal effects on egg and hatching sizes may be most significant under conditions of poor food availability or competition among larvae, where subtle differences in body size confer survival advantages to larger larvae (Hutchings 1991; Blom et al. 1994).

Maternal effects were also detected in the variation of larvae about the mean hatching length, explaining half or more of the total variance in CV at all temperatures except 13 °C. Given that size differences among larvae early in ontogeny are largely carried through development (Chambers and Miller 1995; Chapter 3), or that large hatching larvae may have a corresponding higher growth rate than smaller hatchlings (Rosenberg and Haugen 1982), these maternal differences in dispersion may be important, particularly when considered on a relative size scale. If mortality during the early life history is somehow selective for larval size or growth rate, greater variability in these characteristics among larvae may increase overall survival of the cohort (Pepin 1989; Rice et al. 1993). Consequently maternal differences in the CV of HL, particularly at lower temperatures where dispersion is the greatest overall and maternal effects on individual hatching lengths are strongest, could mean that the survivors represent a non-random female contribution of all the eggs produced by a population. This suggestion is particularly true in the face of the hatching rates observed in this study. I hesitate in extrapolating hatching success results from small static rearing

containers to pelagic eggs in the wild. However my results nonetheless suggest that the pattern of hatching success from different females will vary across temperatures and thus affect the percent contribution of each female to the pool of larvae in a population (a result similar to Buckley et al. 1991). Furthermore, it is possible that differential survival of embryos among females may influence the observed maternally-derived variability in hatching length if embryonic mortality is selective of size. For example, if smaller embryos have a lower probability of survival, a female producing eggs with overall poor survival would produce hatching larvae that are larger on average.

Preserved larvae were used as the units of study for all analyses of HL because back-calculation of fresh lengths would have increased the error associated with those lengths. This lack of correspondence between fresh and preserved lengths of larvae is an aspect that is often overlooked when shrinkage correction factors are applied without considering the effects of preservation on the individual larvae (Pepin et al. 1998). This effect may have increased the error variance in my analyses of HL. In addition, because large larvae shrank to a greater extent in absolute terms, the use of preserved lengths in my analyses may have underemphasized the variance attributed to female effects. This effect may be particularly true at the lower temperatures where the CVs and mean HLs were largest, and consequently relative differences in HL among larvae would be greater if fresh lengths were used.

Overall, the maternal contribution to development time was small both across and within temperature treatments, as has been found in other species (Knutsen and Tilseth 1985). The overriding influence of temperature on development has been well

documented (Pauly and Pullin 1988; Duarte and Alcaraz 1989; Pepin 1991), and egg size generally has greater influence on the duration of the yolk-sac stage than the egg stage (Knutsen and Tileseth 1985; Pepin et al. 1997). Within temperature treatments, the strongest influence on development time was experimental error. A strong influence of experimental error was also found for the CVs of HL (34% variance) and DT (53%). Differences among replicates could possibly be due to minute differences in the temperature or lighting experienced by each rearing container. I could have better quantified this variance had I used a randomized block design for the placement of rearing containers, allowing me to block the variance enhancing effects of spatial heterogeneity within treatments (as per Chambers et al. 1989). Furthermore, my results highlight the importance of high levels of replication when accurate and precise estimates of dispersional and distributional properties of a population are of interest, particularly given their sensitivity to sample size.

Aside from the immediate survival differences among eggs of different females due to differing hatch rates and sizes at hatch, I do not believe that the consequences of maternal variation (particularly the non-genetic components considered here) extend far into the juvenile stage (as per Chambers and Leggett 1992), and I suspect that multi-generational effects are unlikely. This result is common in non-livebearing animals, where developmental plasticity among progeny erodes the initial phenotypic differences of maternal origin by the time maturity is reached (Bernardo 1996a). In this study, variance ascribed to maternity was greatly reduced when eggs were compared to larvae (with further reductions predicted for later in ontogeny). Furthermore maternal effects

in the larval stage were highly dependent on temperature, and consequently initial differences in body size (and growth rate), that may influence the growth trajectories of larvae (Chapter 2), need not be ascribed to maternal differences. In general, I have shown that a little over half of the variance in hatching length among larvae can be explained by a combination of maternal effects and covariance with development time, but the influence of each factor differs in a systematic way depending on the rearing temperature. Maternal effects may influence recruitment by the timing, number and quality of eggs produced over the spawning season (Kjesbu et al. 1995; reviewed by Solemdal 1997). However, the potential for maternally-derived differential survival of eggs and larvae will be highly dependent on the environment that they encounter, and most prominent under conditions of slower development or poor growth (Hutchings 1991; Marteinsdottir and Able 1992; Blom et al. 1994).

Table 4.1 Temperatures for the various incubation treatments (mean, SE, range)

Treatment	N	Mean (°C)	SE	Range (°C)
5.5 °C	37	5.75	0.03	0.8
7 °C	27	7.07	0.02	0.4
9 °C	21	9.12	0.03	0.8
11 °C	19	11.15	0.03	0.6
13 °C	19	12.46	0.04	0.7

Table 4.2 Information on females (weight, length) and the batches from which the eggs were taken.

Female	Weight (g)	Length (cm)	Batch volume [1] (mL)	Viability[2] (%)	Egg diameter (mm)[3] mean (SE)
A	489	36.5	50	55	0.86 (0.002)
B	589	34	30	71	0.82 (0.002)
C	699	34	20	89	0.79 (0.002)
D	625	33	10	72	0.90 (0.005)

[1]- the volume of eggs produced by the female on the day in which eggs were taken

[2]- calculated as the percentage of unfertilized eggs out of 50 which were capable of being fertilized. Viable eggs float in sea water, are spherical and colourless.

[3]- 100 eggs measured per female, except female D (59 eggs measured)

Table 4.3 Results of analysis of variance for mean development times[1] and coefficients of variation[2], with estimated variance components.

Source	d.f.	MS (type III)	F	P	Variance component	%
Mean development time:						
Female	3	0.017	1.29	0.30	0	0
Temperature	4	8.24	618	<0.0001	2.31×10^{-2}	98.6
Female*Temperature	11	0.012	0.94	0.52	8.23×10^{-5}	0.35
Error [3]	33	0.013			1.65×10^{-4}	0.7
Replicate (female) [4]					8.92×10^{-5}	0.38
Total					2.34×10^{-2}	100
CV development time:						
Female	3	0.002	0.70	0.56	0	0
Temperature	4	0.013	4.88	<0.005	7.85×10^{-6}	12.3
Female*Temperature	11	0.007	2.50	0.02	2.22×10^{-5}	34.9
Error [5]	32	0.003			3.36×10^{-5}	52.8
Total					6.37×10^{-5}	100

[1] Development times were log10-transformed

[2] CV's of development times were arcsine-transformed

[3] The error term represents differences in DT among replicates in the ANOVA but represents variation within replicates in the calculation of components

[4] Replicates nested within female effects were not included in the ANOVA as the analysis was for replicate means.

[5] The error term represents differences in CV among replicates

Table 4.4 Results of analysis of variance for the mean and coefficient of variation[1] of hatching length in replicate cultures, along with estimated variance components.

Source	d.f.	MS (type III)	F	P	Variance component	%
Mean length at hatch:						
Female	3	8.31	77.7	<0.0001	5.50×10^{-3}	22.2
Temperature	4	1.08	10.1	<0.0001	1.10×10^{-3}	4.40
Female*Temperature	10	0.390	3.65	0.0023	1.90×10^{-3}	7.82
Error [2]	33	0.107			1.61×10^{-2}	65.5
Replicate (female) [3]					1.27×10^{-5}	0.05
Total					2.46×10^{-2}	100
CV length at hatch:						
Female	3	2.89	9.98	<0.0001	3.21×10^{-3}	19.7
Temperature	4	4.08	14.1	<0.0001	5.08×10^{-3}	31.2
Female*Temperature	10	0.611	2.11	0.053	2.51×10^{-3}	15.4
Error [4]	32	0.289			5.50×10^{-3}	33.8
Total					1.63×10^{-2}	100

[1] CV's of HL were log10-transformed to meet the assumptions of the analysis. This provided greater normality and homogeneity of residuals than the arcsine-transform, which is recommended for ratios (Sokal and Rohlf 1981).

[2] The error term represents differences in HL among replicates in the ANOVA, but represents variation within replicates for the variance components.

[3] Replicates nested within female effects were not included in the ANOVA as the analysis was for replicate means.

[4] The error term represents differences in CV among replicates.

Table 4.5 Variance components for development time (DT) and hatching length (HL) estimated using individual larvae at each temperature treatment

		Female	Explained Variance in DT (%)			Total
Temperature	N	(P-value)	Female	Replicate[1]	Error[2]	Variance ($x10^{-4}$)
5°C	1286	0.21	5.4	57.5	37.1	5.23
7°C	1678	0.17	16.1	28.8	55.1	1.64
9°C	1723	0.51	0.0	45.3	54.7	2.62
11°C	1002	0.38	9.6	24.8	65.6	1.64
13°C	962	0.41	8.8	29.4	61.8	1.53

		Female	Explained Variance in HL (%)			Total
Temperature	N	(P-value)	Female	Replicate[1]	Error[2]	Variance ($x10^{-2}$)
5°C	934	<0.0001	33.9	2.2	63.9	3.91
7°C	1615	<0.0001	46.8	2.2	51.1	3.30
9°C	1667	0.0003	45.9	3.9	50.2	2.27
11°C	962	0.004	28.6	1.6	69.9	1.80
13°C	900	0.044	15.0	7.0	77.9	1.88

[1]- Replicates nested within female effects; $P<0.002$ for all cases.

[2]- Variation among larvae, within replicates

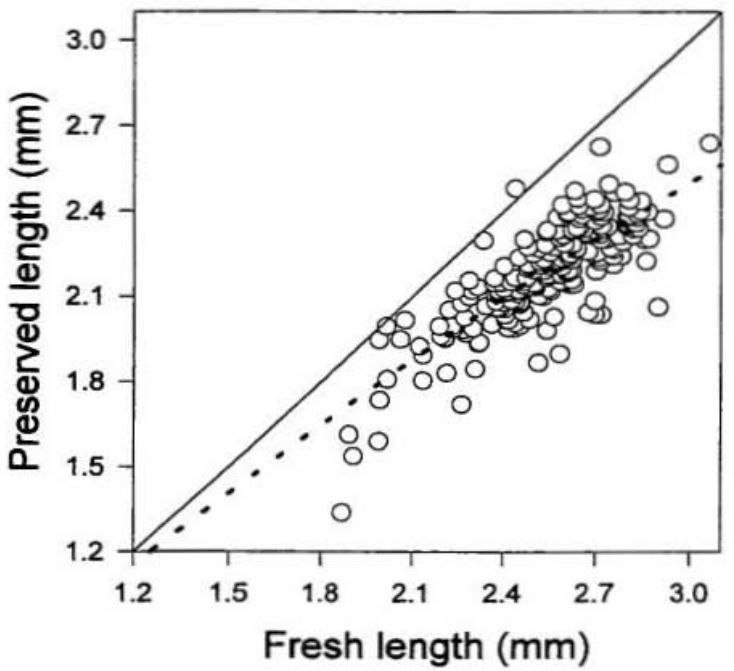


Figure 4.1. Effects of formalin preservation on the standard length (mm) of yellowtail flounder larvae at hatch. The dashed line represents the fit of the nonlinear model, β_0=6.32 (ASE=1.17), β_1=0.17 (ASE=0.04), R^2=0.66, P<0.0001. The solid line represents a perfect correlation between fresh and preserved lengths.

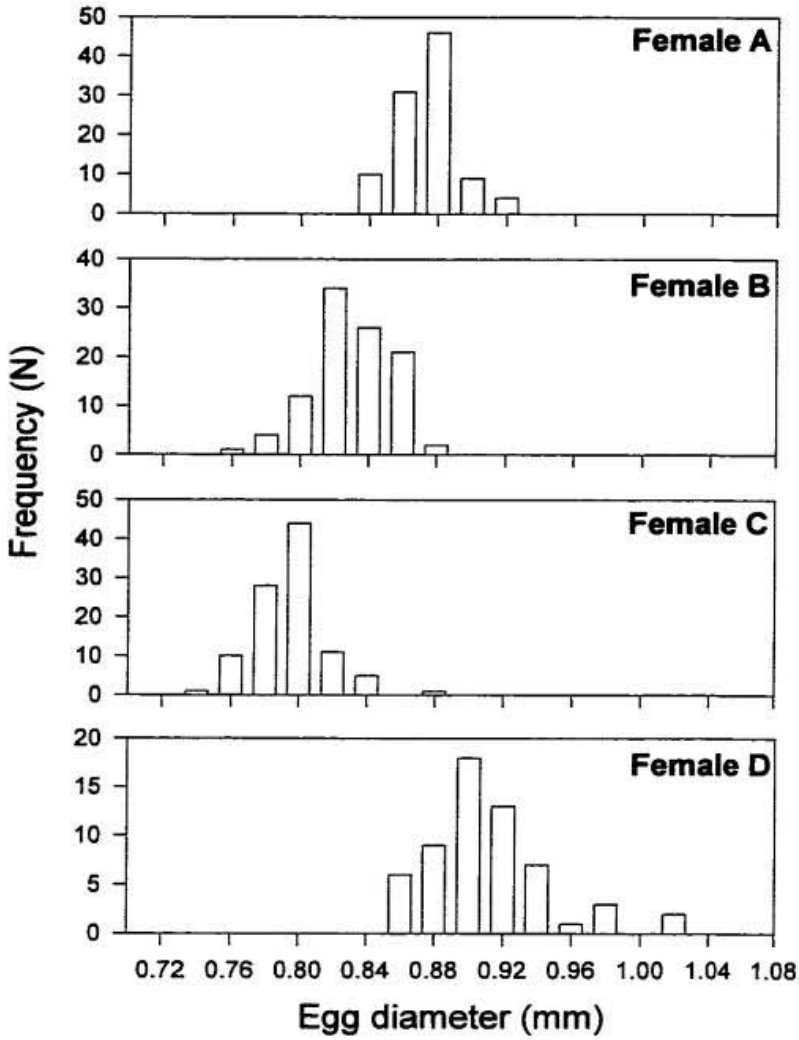


Figure 4.2 Egg diameter (mm) frequency distributions for each of the four experimental females.

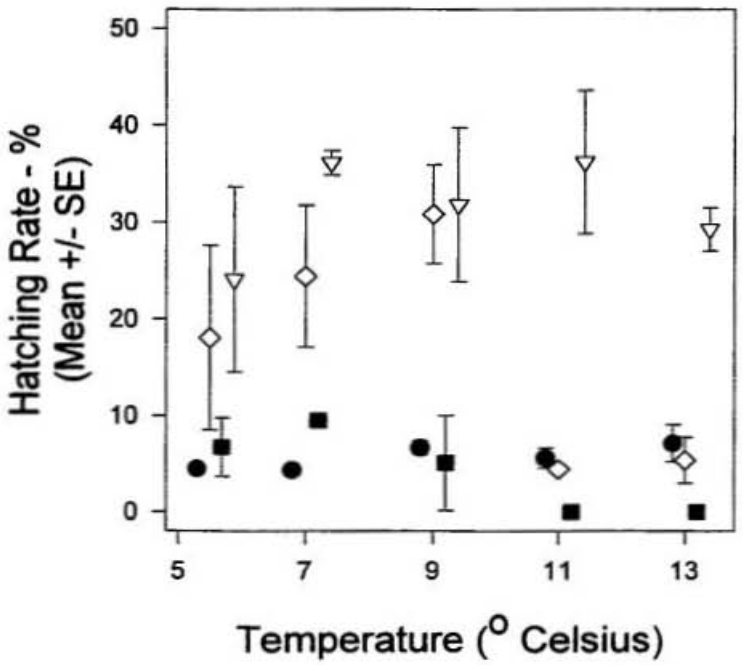


Figure 4.3 Percent hatching rate (mean ± SE) for eggs from each female at each rearing temperature. Hatching rate is calculated as the percentage of viable eggs (spherical, translucent, floating) that produced live larvae. Female A (●), female B (◊), female C (■), and female D (▽).

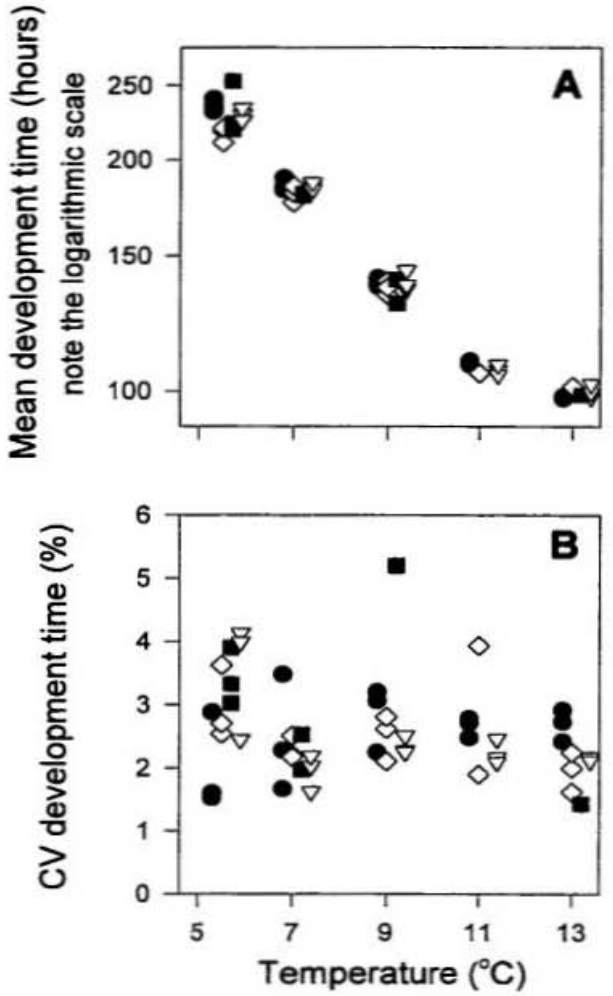


Figure 4.4 a) Mean development time (hours) of replicate batches of eggs from each of the four females, reared at five different temperatures. Female A (●), female B (◊), female C (■), and female D (▽). b) Coefficient of variation of development time of replicate batches of eggs. Data for individual replicates are presented to better show the degree of inter-replicate variation (experimental error). Note that the points for the separate females are offset at each temperature for display purposes only.

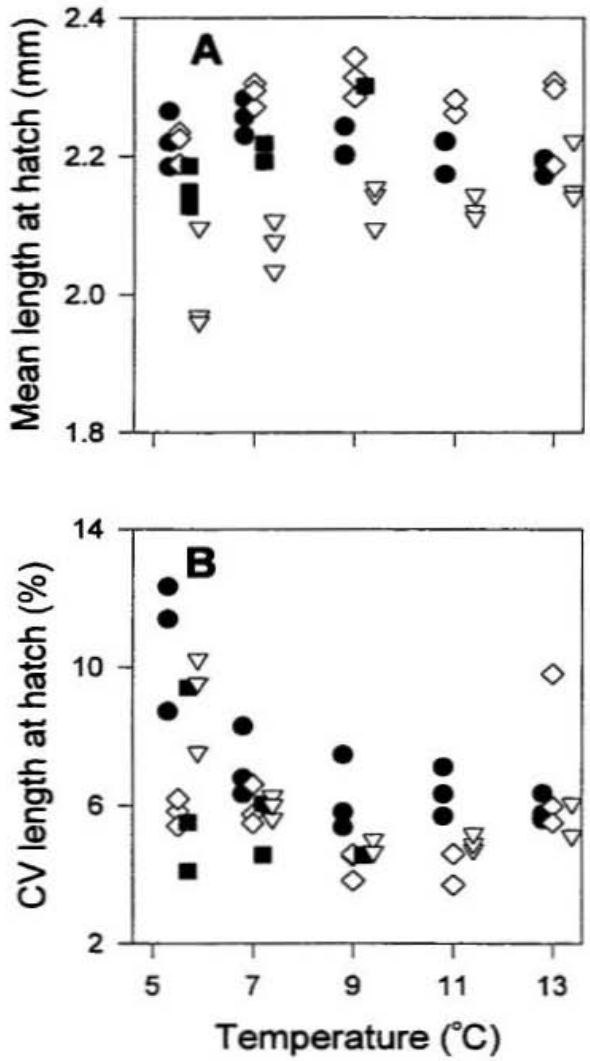


Figure 4.5 a) Mean length at hatch (mm) of replicate batches of eggs from each of the four females, reared at five different temperatures. Female A (●), female B (◊), female C (■), and female D (▽). b) Coefficient of variation of hatching length of replicate batches of eggs. Data for individual replicates are presented to better show the degree of inter-replicate variation (experimental error). Note that the points for the separate females are offset at each temperature for display purposes only.

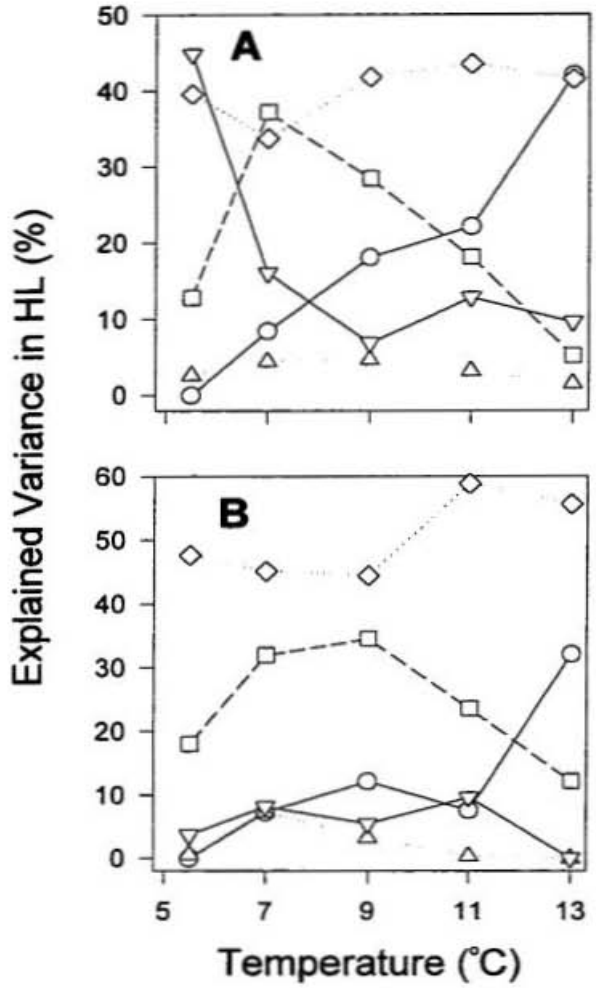


Figure 4.6 a) Variance components for the among individuals variance in hatching length at each of the rearing temperatures. Explained variance is partitioned into components for the covariation with development time (o), maternal effects (□), experimental (replicate) error (Δ), interaction between development time and maternal effects (▽), and residual variance (i.e. among individuals within-replicates) (◇). b) Same as above with the exception that equal numbers of larvae from each female were used in this analysis at each temperature. Larvae were randomly sampled (regardless of replicates) from all of the larvae produced by each female (at each temperature), until the number of larvae used in the analysis was equal among females.

Chapter 5
Synthesis

Empirical and Theoretical Aspects of Variability in Growth and Development Rates of Marine Fish Early Life Stages

Abstract

This chapter summarizes the factors that interact to affect individual timing of early life history transitions in marine fishes. The results presented in the previous chapters demonstrate that there is considerable scope for variability in stage durations and transition lengths among individuals. However, much of this variability appears to be generated in a predictable manner throughout ontogeny. In support of this idea, results from an empirical literature review on the individual-level timing of hatching in marine fishes are presented and compared to those found in Chapter 2 for metamorphosis. Variability in transition lengths appears to be affected by similar factors for eggs and larvae. Stage durations of both stages are also affected in similar ways by temperature and body size. Variability in stage durations increases exponentially with mean duration, and the relationship is identical for eggs and larvae, suggesting that individuals diverge in a continuous manner throughout ontogeny. This pattern also suggests that some degree of serial development autocorrelation must exist (i.e., a better developed individual on one day is more likely to be better developed the next). Using a simple analytical model, I show that autocorrelation in the size of individuals can

occur even when different growth rates are randomly distributed in a population. Serial autocorrelation in individual growth rates acts to strengthen the persistence of size autocorrelations in time. Overall the results presented in this chapter support the idea that small initial differences among individuals can have lasting effects on individual life histories and chances for survival.

Introduction

A recurring theme of this thesis is that considerable variability exists in the growth and ontogeny of marine fish early life stages. This variability results in plasticity in the timing (age and size) of life history transitions at several levels of resolution (taxonomic, population, cohort and individual levels). Interspecific comparisons of transition sizes and stage durations suggest that large differences may exist in the survival potential of eggs and larvae (Miller et al. 1988; Pepin 1991) resulting in different levels of recruitment variability (Pepin and Myers 1991). At the population or cohort level such an effect of transition timing on recruitment, particularly the impact of stage duration on overall survival, has been demonstrated empirically for several species (Crecco and Savoy 1985; Rice et al. 1987; Bell et al. 1995). In particular, there are a growing number of studies that show that the effects of time (stage duration) on the cumulative mortality of a cohort may be sufficient to explain large differences in recruitment among cohorts (Bell et al. 1995; Campana 1996; Bell 1997). In other words, the number of survivors depends on the amount of time that eggs and larvae are

exposed to the high and variable rates of mortality that occur in the pelagic environment (Dahlberg 1978; McGurk 1986; Pepin 1991). This idea can be formalized as a stage-specific survivorship (l), which is the proportion of individuals that make it from stage a to stage b:

$$(1)\ l(a,b) = \exp-\left(\int_a^b \frac{M(x)}{g(x)}dx\right) = \exp(-Mt)$$

where $M(x)$ is the instantaneous mortality rate, and $g(x)$ is the instantaneous growth rate, both of which are affected by factors (x) that influence the rates. Examples of such factors are temperature and body size (Pepin 1991). The term on the right hand size follows from the inverse relationship between growth rate and stage duration (t). Houde (1987) and Beyer (1989) have explored the dynamics of this simple relationship and demonstrated a large sensitivity of survival to both stage duration and mortality.

Given that the relationship in (1) appears to apply to cohorts and populations (Bell et al. 1995; Campana 1996; Bell 1997), it seems logical that the mechanism also holds for individuals. In such a case the proportion of larvae that survive to stage b in (1) can be considered the probability that an individual will survive over that time interval. It is obvious that if all individuals of a population have identical stage durations, then recruitment for that population will be described by (1), however as I have shown in the previous chapters, individuals cannot be regarded as identical. The belief that individual differences in body size, growth trajectories and transition timing in fish early life stages can explain recruitment variability has resulted in a suite of

studies that have modelled the survival of individuals (Pepin 1988; Rice et al. 1993; Cowan et al. 1996; Paradis et al., *accepted*). Overall these studies have found that individual differences are important, although the strength of the effect may vary (see Paradis et al., *accepted*). Empirical evidence of inter-individual differences in survival potential has been limited due to difficulties associated with following the survival of individuals through time (Miller 1997). Nonetheless, studies utilizing the relationship between otolith size and fish length have shown that size at hatch (Rosenberg and Haugen 1992), and the growth rate of individuals through early life (Post and Prankevicius 1987; Tsukamoto et al. 1989; Hovenkamp 1992; Meekan and Fortier 1996) may determine which larvae survive. An important result of the previous chapters is that the development time (and to an extent transition size) of individuals vary in a relatively predictable manner. Consequently individual survivorship (probabilities) may be predictable across environments.

This chapter summarizes the sources of variability in age and size of individuals at hatch and metamorphosis. I will begin by reviewing the endogenous and exogenous factors that determine the life history of individual fish. In doing so I will draw comparisons between the timing of hatching and metamorphosis at the individual level, and show that variability among individuals is generated at similar rates for hatching embryos and metamorphosing larvae across many species of marine fish. This section is followed by a review of the theoretical aspects of growth variability, which has been summarized by Riska et al. (1984). Using a simple model, I will show that small initial differences in the size of larvae can persist over time, and show how serial

autocorrelation in the growth rate of individuals can exacerbate this effect. This result, combined with the results from the otolith growth increment study in Chapter 3, demonstrate that the fate of individuals, including their chances (probability) of survival, may be determined early during ontogeny.

Variability in Individual Life Histories

The sources of individual variability in transition timing can be summarized generally by three interacting effects: the environment, non-genetic maternal effects, and autocorrelation in the performance of individuals. The environment in which individual embryos and larvae are reared (salinity, temperature, food availability and quality) affects stage durations and transition sizes (Chambers and Leggett 1992; Miller et al. 1996; Chambers 1997; Pepin et al. 1997; Chapters 2, 3, 4). Eggs and larvae are also indirectly affected by temporal and spatial (or geographical) variation in the environment, which impact the size of propagules produced by females (reviewed in Trippel et al. 1997 and in Chambers 1997). Differences in egg size, yolk and oil globule volume exist both among females and among siblings (Chapter 4; Chambers and Leggett 1996), and interact non-linearly with the environment encountered during embryological development to produce variability in hatching size (Chapter 4). Generally these maternal effects are believed to be most prominent at hatch, although they can persist well into the larval period (Chambers and Leggett 1989b, 1992), resulting in a divergence in size-at-age among individuals (Chambers and Leggett 1996). The divergence in growth trajectories often observed among individuals has led

researchers to suggest that individual genetic differences in growth and development rates may be important (e.g. DeAngelis and Coutant 1979; DeAngelis et al. 1993; Gallego et al. 1996). This factor has not been evaluated directly for marine fish eggs and larvae, and only a quantitative genetics study, such as that of Newkirk et al. (1981) for mussel larvae, could judge the importance of genetics to individual differences in performance. Nonetheless, even if no genetic factor affects growth, the multiplicative nature of growth and ontogeny (Fuiman and Higgs 1997) may have similar consequences. This third source of individual variability, namely a cascade of events during ontogeny, whereby the development of a feature depends on development of other features before it, may result in increasing divergence of individual growth trajectories. These differences in growth trajectories are then translated to differences in metamorphic age and length (Chapter 3).

The preceding summary is clearly an oversimplification of the factors that cause individual life histories to differ within a population, but even this simplification has complex interactions among factors. The question is how much of this complexity is relevant to the ultimate distribution of transition ages and sizes, and more importantly, which aspects have the greatest impact on individual survival variability? A common theme of the data presented in Chapters 2, 3, and 4 is that variability among individuals is generated in a relatively predictable and continuous manner. This is manifested in the continuous relationship between mean egg and larval stage durations and the temperature or growth potential of the environment (Duarte and Alcaraz 1989; Pauly and Pullin 1988; Pepin 1991; Chapters 2, 3, 4). The temperature-developmental rate

relationship has also been shown to apply to individuals (Pepin et al. 1997). In addition to environmental effects on mean development time, the variability that surrounds that mean changes predictably with it (Chapter 2; see also Chambers 1993). Based on current information, the response of average transition size to different environments appears to be species specific (e.g. Chambers and Leggett 1992), although recent analyses suggest that this inconsistency may be a result of not considering the entire range of environments encountered by a species (Chambers 1997; Pepin et al. 1997). Within species however, the distribution of individual transition sizes seems predictable as long as environmental (e.g., temperature) and maternal effects, as well as covariance with development time (i.e., growth trajectories), are taken into account (Chapters 3, 4).

In the goal of finding general patterns in the generation of individual life history variability, it may be informative to see if eggs and larvae are affected in similar ways by the factors listed at the beginning of this section. Are hatch and metamorphosis distinct processes as the term "transition" implies (e.g., saltatory ontogeny, Balon (1984)), or are they part of a continuous ontogeny that begins at fertilization, resulting in variability that is generated in a continuous manner throughout early life? To address these issues I have reviewed the literature on egg development time (mean and standard deviation) and hatching length for many species of marine fish, and summarized the data in a similar analysis to that for metamorphosis described in Chapter 2. The review is not as extensive as that for metamorphosis in that the analysis will be limited to the patterns that reflect individual level differences in transition timing. This type of analysis is presently lacking in the scientific literature for marine fish egg development.

Unlike with fish metamorphosis, there are good reviews on the factors that affect the species and population level development times and lengths of hatching larvae (Duarte and Alcaraz 1989; Pauly and Pullin 1988; Pepin 1991; Chambers 1997) and consequently these factors will not be addressed here in any detail.

Data were gathered from a general literature search as in Chapter 2. Basic information consisted of mean or median development time, the standard deviation or range in development times for populations, the mean length at hatch and standard deviation in hatching length. Ranges of development times were converted to standard deviations as per Sokal and Rohlf (1981). Regression and non-parametric correlation (Kendall's τ) analyses were used to evaluate the relationships between temperature and mean development time, as well as mean-standard deviation relationships for development time and hatching length. When more than one observation from a species was included, each point was weighted by the inverse of the total number of data points for that species. Data sources for the review are denoted by an (H) in the literature cited. I have also added the relevant information from the yellowtail flounder experiments (Chapters 3, 4) to the review data to show that these results fit with the interspecific patterns.

Transition lengths

The data from Chapter 2 relating the mean length at metamorphosis (mm) and associated standard deviations are re-plotted in Figure 5.1 along with similar data for hatching larvae from seven species of marine fishes. The log-log relationship for

hatching lengths was weak but statistically significant ($r=0.38$, $\tau=0.42$, $n=92$, slope($\pm$ SE)$=0.81\pm 0.20$, intercept($\pm$ SE) $= -1.10\pm 0.12$). Populations of larvae within species did not show a similar trend. The data for hatching and metamorphic length show a similar tendency for increased dispersion with increasing mean.

In Chapter 4, variance in hatching length of yellowtail flounder eggs was shown to be affected by several interacting factors (e.g. maternal and environmental effects). The interaction of these factors resulted in different levels of hatching length variance for a limited range of mean lengths. When plotted along with other species in Figure 5.1, it is apparent how this variability in dispersion contributes to the weakness of the overall mean-standard deviation relationship (particularly within species). Furthermore it is evident that yellowtail flounder is not the only species to show vast differences in length dispersion for a very limited range of average lengths. This result suggests that variance in hatching, and metamorphic lengths in these species are also likely determined by several factors.

Development time

The data from Chapter 2 relating temperature and age at metamorphosis (days) are re-plotted in Figure 5.2 along with data for the effect of temperature on the development time (days) of eggs from 13 species of marine fishes. Data from the different species are not plotted individually, with the exception of those from yellowtail flounder, in order to minimize the clutter in the figure. These intraspecific patterns (that

generally conform with the overall relationship) are beyond the scope of this individual-level review, and are discussed elsewhere (Pepin 1991; Chambers 1993).

Overall, the temperature dependency of development time is very similar for eggs and larvae (Figure 5.2). Log-transformed egg development time was significantly related to $\log_{10}$(temperature) ($F_{1, 250}$=824.87, P<0.0001) and $\log_{10}$(egg diameters) ($F_{1, 250}$=8.03, P=0.005), with an overall high explained variance (R^2=0.79). This result has been shown previously (Duarte and Alcaraz 1989; Pauly and Pullin 1988; Pepin 1991). The overall relationship for egg development time (DT), with standard errors written below each parameter, is

$$\log_{10}(DT) = 1.991 - 1.255\ \log_{10}(\text{temperature}) + 0.277\ \log_{10}(\text{egg diameter})$$
$$\qquad\qquad (0.046)\quad (0.044) \qquad\qquad\qquad (0.098)$$

The slopes relating temperature to the development time of eggs from fertilization to hatch and larvae from hatch to metamorphosis differ statistically ($t_{df=313}$=2.27, P=0.012), with egg development being more sensitive to changes in temperature than larval development (Chapter 2). This result is similar to that found by Pepin (1991), however the significant difference between the slopes may be a result of the limited number of species used for the relationship at metamorphosis and the overall large sample size that inflated the degrees of freedom for the t-test used in the comparison. It may also be a result of the influence of differences in food availability on variability in the growth rate of larvae for a given temperature (Chapter 3).

The difference in intercepts for the two relationships may reflect a size dependency of development rate as found for eggs (Duarte and Alcaraz 1989; Pauly and Pullin 1988; Pepin 1991). Species with larger eggs will have developmental rates that vary with temperature in a similar manner to the eggs in Figure 5.2 (i.e. the relationship will be parallel to the overall trend), but will be shifted upwards. Although no effect of body size on development time for metamorphosing larvae was found in Chapter 2, this result may largely be due to the limited number of species for which data was available. The calculated intercept for the metamorphic age-temperature relationship was 2.682 (0.144 SE). Assuming that larvae are subject to a similar size dependency in development rate as eggs, it would take a 310 mm (i.e. $10^{2.495}$) individual to produce a relationship with an intercept of 2.682. This is not a possible explanation given that most larvae metamorphose between 7-12 mm (Chapter 2). However it may be more appropriate to scale the difference between eggs and larvae in terms of weight, as rates of metabolism are related to body weight (e.g. Giguere et al. 1988). To do so, weight is assumed to be proportional to length raised to an average power of 3.08 (Pepin 1995), and modal egg diameter is 1 mm (Chambers and Leggett 1996), or ~1 mg dry weight. I will also assume that the size-dependent processes that affect development rate act throughout the larval period, and as a result an average value for the whole period has to be used to compare with the eggs. From Chapter 2, an appropriate average metamorphic length across species is about 10 mm. Based on this figure we can assume that the mean length of larvae averaged over the entire larval period is about 6-7 mm (~250-400 mg). This assumption leads to a two to four hundred fold difference in mass

between eggs and larvae, a difference that is of the correct order to explain difference in the intercept for the development time relationship. Although this explanation is highly speculative, the overall pattern in Figure 5.2 suggests that developing eggs and larvae are subjected to similar temperature and possibly size-dependent rates of ontogeny.

Hatching and metamorphosis are also very similar in how variability surrounding mean development time is generated (Figure 5.3). The mean-standard deviation relationship for egg development time for 6 species (r=0.92, τ=0.77, n=104, slope(± SE)=1.53± 0.06, intercept(± SE)= -1.10± 0.12) did not differ in slope from that for metamorphosis ($t_{df=289}$= 1.02, P=0.16). As with metamorphosing larvae (Chapter 2), the relationship for hatching eggs is consistent within and among species. Furthermore, the overall relationship spans two orders of magnitude for mean development time, and almost three orders for standard deviation suggesting that a common mechanism is generating this variability. Such a continuous pattern is expected to be more characteristic of a continuous ontogeny rather than a punctuated development characterized by a series of discrete events (e.g., Balon 1984). This last speculation is corroborated by the data of Pepin et al. (1997) on cod (*Gadus morhua*) egg development, who estimated mean development time and standard deviation for embryos at five developmental stages preceding and including hatch, and at yolk absorption (Figure 5.3). These data fit in reasonably well with the overall relationship for hatching and metamorphosis.

Discussion of Empirical Trends in Individual Early Life History Variability

The strong and consistent mean-standard deviation relationship for development time among species and populations (Figure 5.2) is in stark contrast to the relationship for transition length (Figure 5.1). As discussed in Chapter 4, length at hatching is affected by complex interactions between egg size (maternity), temperature and development time. As a result, for a single species, mean length and its standard deviation are not expected to covary in a predictable manner given that variance in hatching length stems from different sources under different rearing conditions. This is not the case for development time as maternal effects had only a relatively minor role in determining variance. For pre-metamorphic larvae, individual lengths at metamorphosis appear to be very sensitive to the growth of larvae during a relatively short interval prior to transformation (Chapter 3). In contrast mean development time and the variability around it stem from growth over the entire larval period (Chapter 3). Thus, metamorphic age is an integration of growth processes occurring over a wider time span than those for metamorphic length, possibly resulting in less stochasticity (i.e., sensitivity to small initial differences), and greater predictability in the manner in which variance will change with increasing means.

Although the mean-standard deviation relationship for transition lengths did not hold intraspecifically, there was an overall positive association interspecifically. As pointed out in Chapter 2, the slope and intercept of this relationship are similar to those for development time, suggesting that the two processes may be linked. This result is quite plausible given that the two variables are related by the growth process, and in fact

the overall relationship for transition length may represent a scaling to average development times (and associated variances). As pointed out previously, among species, larger organisms take longer to develop than smaller ones, *ceteris paribus*. However this relationship is weak when considered intraspecifically (Miller et al. 1995; Pepin et al. 1997), and as a result species with larger transition sizes will have longer development times *on average* only. From Figure 5.3, it follows that these longer transition times will be accompanied by higher levels of individual (age) variability that may be translated to more variable sizes.

The possible origins of the mean-standard deviation relationship for transition age have been discussed in Chapter 2, and are only briefly summarized here. It is generally accepted that the growth and ontogeny of fish early life stages are multiplicative processes, and both are tightly linked to one another (Fuiman and Higgs 1997). By "multiplicative processes", I mean that the size or developmental stage that an individual has achieved by a certain time will affect future rates of growth and development (i.e., development builds upon the differentiation that has already occurred). As a result of this multiplicative nature, we would expect that the propagation of variability would also occur multiplicatively, as in Figure 5.3. Furthermore we would predict that development times should be log-normally distributed, and become increasingly skewed with increases in means and standard deviations (see the arguments given in Chapter 2).

This result can have major implications for recruitment if individual survival is determined as in equation (1). The reason is that the mean is a poor estimator of central

tendency in log-normal distributions, overestimating the response of the majority in the population (Aitchison and Brown 1976). This result means that the stage duration of the majority of the population (i.e. the median) will be shorter than the mean, resulting in higher survivorship for those individuals than otherwise expected. However, a log-normal transition age distribution also means that a few individuals will have disproportionately long stage durations. Given that survivorship decreases exponentially with time (1), these individuals will have very slim chances for survival relative to the majority. This effect will become even more pronounced with increasing average development time, as standard deviation (Figure 5.3) and skewness of the distribution increase. This effect may explain why selective mortality acting on individual growth rates is most pronounced under conditions of poor growth (e.g. Post and Prankevicius 1987; Meekan and Fortier 1996). In other words we are most likely to see the selective mortality of the 10% slowest growing members of a cohort when that 10% differs most from the rest.

The multiplicative nature of growth and development also suggests something that is much less well studied in marine fish early life stages, namely that small initial differences among individuals are propagated though time. This suggestion means that differences in body size persist (i.e., serial size autocorrelation), and that growth and development rates are likely also autocorrelated in time. The mean-standard deviation relationship for transition ages (Figure 5.3) suggests that the degree of these autocorrelations is similar among species, populations and life history stages. In Chapter 3, growth rates of larvae during the middle portion of larval life were shown to

be serially autocorrelated, with values ranging from 0.54 to 0.70 (rank correlations) when considered over a 2-week interval. Similarly, Chambers and Miller (1995) found rank correlations of about 0.7-0.8 in larval Atlantic menhaden (*Brevoortia tyrannus*) at a 12-day measurement interval (calculated from data presented in an appendix to their paper). Imsland et al. (1998) have assembled individual growth data from laboratory studies of juvenile turbot (*Scophthalmus maximus*) and halibut (*Hippoglossus hippoglossus*) and calculated an overall growth rank correlation of 0.4 for two-week intervals between measurements. Similar growth autocorrelations are also apparent in data for larval turbot (Rosenberg and Haugen 1982) and shortbelly rockfish (*Sebastes jordani*) larvae and juveniles (Laidig et al. 1991). Gallego et al. (1996) found that the majority (66%) of the short-term (~daily) variability in larval herring (*Clupea harengus*) growth rates could be explained by past growth history, while short term environmental variability had only a small effect (<3% explained variance). Overall these studies suggest that intermediate levels of short term (daily, weekly) growth autocorrelation occur during the early life stages of many marine fishes, confirming the predictions made based on the mean age-standard deviation relationship.

Based on the relationship in Figure 5.3 and the arguments presented previously, we would expect to find egg development rate autocorrelation similar to that described above for larval growth. Unfortunately, unlike larval fish that provide an accessible record of their growth rates on their otoliths, individual eggs must be reared in isolation in order for development rate to be estimated. Furthermore estimation of a rate at several times during ontogeny requires that egg development be quantified regularly.

Pepin et al.'s (1997) study of cod is the only one to have done so on individual eggs. Unfortunately the majority of ontogenetic stages that were used to describe development occurred over a very short period of time, and because egg development was scored on a relatively coarse (daily) basis, rank correlations were not informative (*unpublished data*).

Another important finding of the otolith growth increment study in Chapter 3 is that the degree of growth autocorrelation varies temporally over the larval period, and is strongest at the mid-point of larval life when growth rates are expected to be greatest (i.e. at the inflection of the sigmoidal growth curve observed by Bertram et al. (1997), and proposed earlier by Zweifel and Lasker (1976)). Furthermore, the data from Chambers and Miller (1995) indicates that the strength of the correlation decays as the time interval between measurements is increased, implying that the performance (growth) of larvae is not necessarily consistent over extended periods of time. Nonetheless even small differences in size and growth over short time spans can have lasting effects on the rank size of larvae. This finding was exemplified in the correlated size ranks of larval yellowtail flounder larvae even in the absence of growth autocorrelation (Chapter 3). When growth autocorrelation was present, serial body length autocorrelations were even stronger (a result similar to Chambers and Miller (1995)).

The following section explores the theoretical basis of serial autocorrelation in growth rate and its effect on size autocorrelation. I will show that size autocorrelation can occur, at least for a period of time, in the absence of correlated growth. Moreover,

growth autocorrelation strengthens the serial correlation in body size and causes it to persist for a longer period of time than it would otherwise. These results will be used to show that small differences in the size or growth of larvae occurring very early during ontogeny can impact the timing of later events (e.g., metamorphosis) and may affect individual survival probabilities. Although the discussion focuses on the growth of larvae, the concepts can easily be extended to the growth of embryos. Given that growth and development are very tightly linked processes (Fuiman and Higgs 1997) autocorrelations in the size and growth of eggs and larvae can also be regarded as autocorrelations in ontogeny and developmental rate.

Theory Behind the Persistence of Individual Size Ranks Through Time

The otolith growth increment analysis presented in Chapter 3 revealed strong correlations in the length of larvae over time that occurred even when growth autocorrelations were small. It is obvious that the amount of serial autocorrelation in body size is time-dependent, such that at very short intervals (on the order of minutes or hours), successive measurements of body size will be strongly correlated. The question is at what rate does this correlation decay over time, and what effect does growth rate autocorrelation play in limiting this decrease?

Serial autocorrelation between lengths can be analyzed in terms of a contribution from variance in length gains (resulting from variance in growth rate over a period of time) and a contribution from covariance in gains (i.e. serial autocorrelation in growth rate). Riska et al. (1984) have formalized this relationship in an analysis of the

theoretical aspects of correlated growth, which is presented below. The model is structured in terms of gains in length (i.e. the amount of length acquired over a period of time), where the initial length of larvae plus the sum of the gains over a fixed period equals the length of the larvae at the end of that period. Using length gains rather than growth rate in the equations means that a growth model does not have to be defined. This aspect is useful given that many different growth models (additive, proportional, logistic, Gompertz) have been applied to the growth of larvae (Zweifel and Lasker 1976; DeAngelis et al. 1993). Furthermore larvae of a single species can display different growth patterns, depending on their nutritional state (Jenkins 1992). The model for autocorrelated growth is further simplified by not explicitly including hatching length, although it can implicitly be considered as the length gain occurring from fertilization (assuming zero length) to hatch.

Given that length gains are additive, the variance surrounding these gains will be additive as well. When two quantities (a and b) possessing variance are added to one another, the variance (var) of their sum can be expressed as:

(2) $\text{var}(a+b) = \text{var}(a) + \text{var}(b) + 2\text{cov}(ab)$

where $\text{cov}(ab)$ is the covariance between a and b, and is equal to $\rho(\text{var}(a)\cdot\text{var}(b))^{0.5}$, where ρ is the parametric or "true population" correlation coefficient.

Turning to the autocorrelation in length, if length gains 1 through N contribute to the length of larvae at time 't' (S_t), and length gains 1 through N plus gains N+1 through

M contribute to the length at time '$t+x$' (S_{t+x}), then the correlation between S_t and S_{t+x} is:

$$(3)\ r_{t,t+x} = \frac{\sum_{i=1}^{N} \mathrm{var}(G_i) + 2\sum_{i=2}^{n}\sum_{j=1}^{i-1} \mathrm{cov}(G_i, G_j)}{\sqrt{\mathrm{var}(S_t)\,\mathrm{var}(S_{t+x})}} + \frac{\sum_{j=1}^{N}\sum_{N+1}^{M} \mathrm{cov}(G_i, G_k)}{\sqrt{\mathrm{var}(S_t)\,\mathrm{var}(S_{t+x})}}$$

where G_i is the gain in length during time period i. Despite a common denominator, the two terms have been separated in order to consider the effect of each of the numerators. The numerator in the first term has the same form as equation (2) except that it is summed over several "gains", and is equal to the variance in length at time t ($\mathrm{var}(S_t)$). As a whole, the first term represents the portion of the correlation '$r_{t,t+x}$' that occurs as a result of the growth shared by S_t and S_{t+x}. The variance in S_{t+x} depends on the variance in size generated up to time t (i.e. $\mathrm{var}(S_t)$) plus the variance added during growth from time t to time $t+x$. This effect can be better exemplified by assuming that growth is uncorrelated in time, such that $\Sigma\mathrm{cov}(G_i, G_j)$ and the second term of equation (3) are equal to zero, reducing it to

$$(4)\ r_{t,t+x} = \sqrt{\frac{\mathrm{var}(S_t)}{\mathrm{var}(S_{t+x})}}$$

This result is significant because it implies that in the absence of growth autocorrelation, length may still be autocorrelated depending on two interacting factors, namely the time interval between measurements and the variance in the growth rate of larvae. As a

simple example, if we assume that larval growth is additive such that growth rate is independent of size (i.e. $dS/dt=g$, where g is constant for an individual), then the length of larvae at a later time can be written as

(5) $S_{t+x} = S_t + gx$

Within the population, if S_t is normally distributed [~N(S_t, var(S_t)] and so is growth rate [~N(g, var(g)], then the mean length at time $t+x$ in the absence of growth autocorrelation will be as written in (5), and the variance in length at time $t+x$ will be

(6) $\text{var}(S_{t+x}) = \text{var}(S_t) + x^2 \bullet \text{var}(g)$

If these values for var(S_t) and var(S_{t+x}) are inserted back into (4), the inverse relationship between serial size autocorrelation and growth rate variability and time becomes apparent. As the time interval (x) is widened, individuals have more time to diverge from one another, effectively reducing the correlation. The fact that this term is squared suggests a particular sensitivity to the time between measurements. At its lower limit, if x is very small (on the order of minutes or hours), then lengths at adjacent times will be highly correlated. The same is true if there is no variance in growth rate over the time interval x (i.e. all individuals growing at the same rate), as var(S_{t+x}) will depend only on initial variability in length. This appears to be the case in a study of laboratory reared juvenile turbot where initial size ranks were maintained over several months as a result of nearly parallel individual growth trajectories (Imsland et al. 1996). However if the variance in the instantaneous growth rate is large, individuals will diverge in a very

short period of time reducing the length autocorrelation. Hallaråker et al. (1995) show such an effect in juvenile halibut (*Hippoglossus hippoglossus*) where lower size rank correlations occurred in treatments with greater amounts of individual growth variability. It is important to note that the dependence of $r_{t,t+x}$ on x and var(g) will vary with the model used to describe larval growth, however there will always be an inverse relationship between these variables.

The second term in (3) represents the effect of growth autocorrelation on the correlation between S_t and S_{t+x} (i.e. when size gains are correlated). If gains covary in a positive manner, the overall numerator in (3) increases resulting in a higher correlation in body lengths over time. This growth pattern is termed depensatory or divergent, and results in an increase in serial length autocorrelation, as well as a large increase in the rate at which variance in length is generated as can been seen from (2). On the other hand if the second term in (3) is negative, and growth is compensatory (e.g. Bertram et al. 1993) such that initially fast growing individuals become the slower growing ones, the correlation between lengths over time will weaken faster than if no covariance in growth existed. Furthermore, as Riska et al. (1984) point out, compensatory growth is the only mechanism that can reduce the variability in length of same aged larvae.

Conclusions

The theoretical considerations of size autocorrelation have shown that genetic differences in growth rate (e.g. Gallego et al. 1996) need not be invoked to explain correlations over time. The fact that developmental processes build upon one another in

a multiplicative fashion means that small differences among individuals will widen over time. Even in the absence of autocorrelations in growth rate, the size of larvae will be correlated for a period of time. This autocorrelation may explain why maternally derived differences in hatching length (Chapter 4; Chambers and Leggett 1996) can persist into the larval stage, and despite decreasing in importance over time, affect the timing of metamorphosis (Chambers and Leggett 1989b, 1992). Initial differences in hatching length (although not necessarily maternally derived) have been shown to persist temporally, determining which larvae survive early life (Rosenberg and Haugen 1982). Serial growth autocorrelations serve to increase the autocorrelation in size as is apparent when different portions of larval life are considered in the yellowtail flounder data (Chapter 3).

This result raises an important point, namely that growth autocorrelations do not have to occur over an extended period to have lasting effects on size autocorrelation. In fact it may be uncommon for larvae to grow relatively faster than others for an extended length of time. Chambers and Miller (1995) show that the autocorrelation in short term (3-day) growth decreases rapidly as the interval between measurements is increased for larval Atlantic menhaden. Using the data that they provide in an appendix, I estimated variance components for short term growth rates of individuals from two cohorts (methods for variance component estimation are given in Chapter 4). The total variance in growth rates was 0.3527, of which no significant portion could be ascribed to differences among cohorts. Variance in growth rate among individuals within a cohort explained 16.9% of the total variance, and the major portion of the variance (83.1%)

was explained by growth variability within individuals. A similar result was found when variance components were estimated for the data on yellowtail flounder growth increments presented in Chapter 3. The total variance in growth rates was 0.7296, 4.9% of which was explained by differences among rearing aquaria, the remaining portion (95.1%) was due to within-individual variability.

Jointly, these results suggest that the majority of growth variation occurs within individual growth trajectories, and that differences among trajectories measured over short intervals (days) are very small when one considers growth over the entire larval period. Nonetheless, these short term autocorrelations may be sufficient to create size differences among common age larvae that persist to affect metamorphic age (Chapter 3). This result means that small differences in hatching length and/or individual growth rates early during ontogeny may determine the chances for survival of an individual as dictated by equation (1). Furthermore the power law relating mean transition age and its variance, along with the log-normal distribution that it implies, suggests under conditions of slow development (poor growth) there will be greater time for individuals to diverge and consequently initial differences will be even more important in determining the survivors.

This chapter has given much importance to development time as a determinant of the survival of individuals through the larval period. This emphasis stems largely from the observation that stage duration can explain a large proportion of observed recruitment variability (Bell et al. 1995; Campana 1996; Bell 1997). However it is important to re-iterate the direct and indirect roles that transition sizes and the size of

larvae at common ages can have on survival. Although recent theoretical work has suggested that size-selective mortality in larval fish may be less important than previously thought (Paradis et al. 1998, *accepted*), the size of larvae prior to metamorphosis may affect their chances for future growth and indirectly affect survival as a result of larval stage duration (Chapter 3). An example of such a size-dependent growth factor is prey niche breadth which may widen with larval size (Pepin and Penney 1997). Furthermore, body size may be most important in determining survival after metamorphosis, during the demersal juvenile stage. Meta-analyses have shown that demersal (juvenile) stages of marine fishes are governed by density-dependent processes (Myers and Cadigan 1993a,b). In those cases body size may determine the competitive ability of individuals. As an example, the size of juveniles at settlement may determine territory size which has been shown to affect post-settlement growth (Tupper and Boutilier 1995).

Overall I have shown in this thesis that the timing of early life history transitions are affected by multiple sources of variability. In Chapter 2, I presented an empirical review that highlighted the need for a better understanding of the timing of metamorphosis in marine fishes at the individual level, and incited the experiments in Chapter 3. These experiments demonstrated the importance of individual growth histories in determining the age and length of larvae at metamorphosis. In particular, metamorphic age becomes predictable early during larval development, suggesting that events associated with hatching or occurring soon after can have lasting effects on individual life histories. In a subsequent experiment, I found that the size of larvae at

hatching was affected by an interaction of maternal, individual egg, and temperature effects. In the current chapter, I have shown that these initial individual differences can have lasting effects on how individuals rank relative to one another (especially if growth rate is autocorrelated), and that divergence among individuals may begin soon after fertilization. Overall this result means that even if recruitment is not set during the "critical period" that accompanies feeding initiation (Cushing 1990), events early in a marine fish's life (its egg size, the temperature at which it was raised, the time it took to develop as an embryo, etc.) can set the stage for its chances for survival weeks or months later.

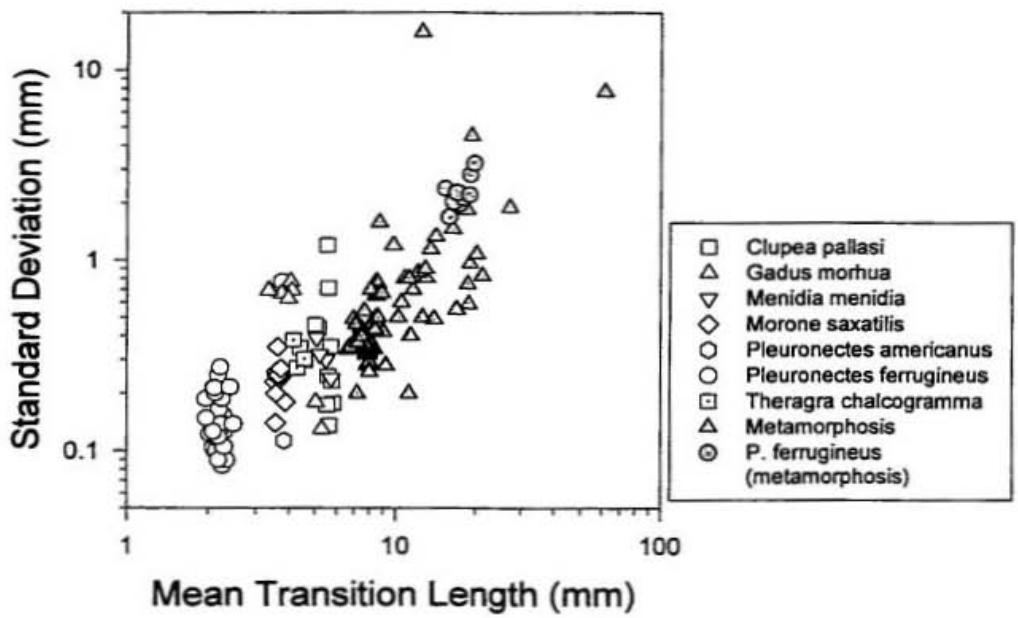


Figure 5.1 Inter- and intraspecific relationship between mean transition length (mm) and standard deviation (mm). Data for hatching larvae are displayed using different symbols for each species. Separate species are not displayed for data regarding metamorphosis (see Chapter 2 for these details), with the exception of data for metamorphosing yellowtail flounder (from Chapter 3).

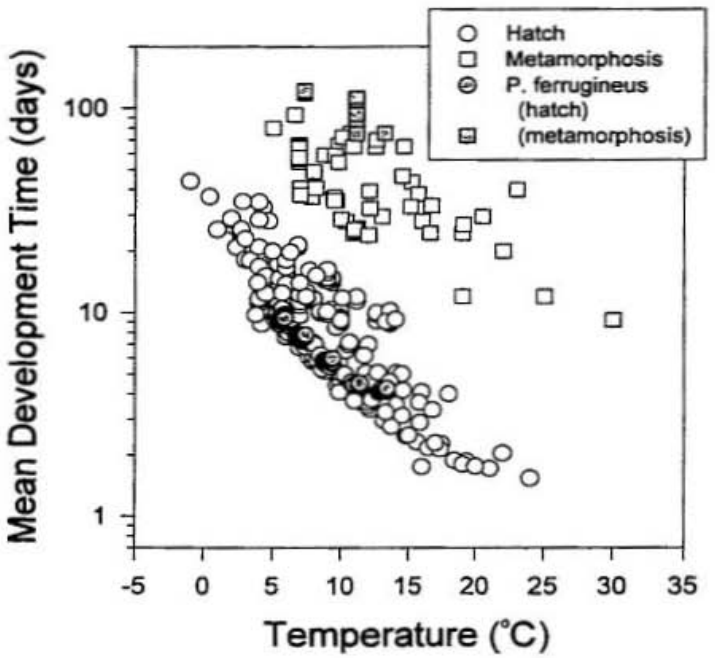


Figure 5.2 Relationship between temperature (°C) and mean stage duration (i.e., development time) (days). Separate species are not displayed for data regarding hatching or metamorphosis (see Chapter 2 for these details), with the exception of data for yellowtail flounder (from Chapters 3 and 4).

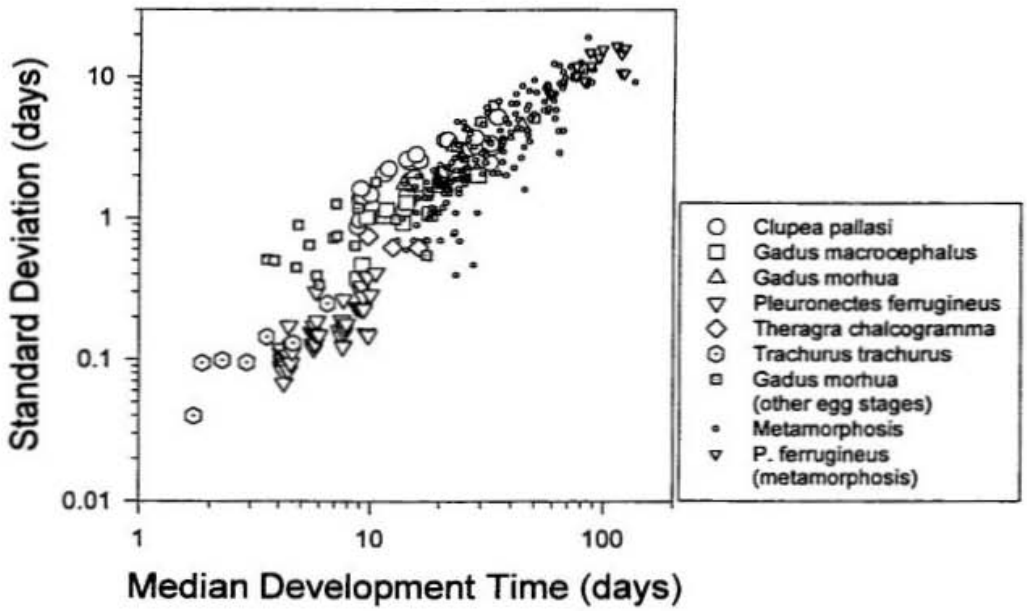


Figure 5.3 Inter- and intraspecific relationship between mean stage duration (i.e., development time) (days) and standard deviation (days). Data for hatching larvae, and other egg developmental stages (for cod), are displayed using different symbols for each species. Separate species are not displayed for data regarding metamorphosis (see Chapter 2 for these details), with the exception of data for metamorphosing yellowtail flounder (from Chapter 3).

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Appendix 1. Summary of the data included in the empirical review of metamorphosis in marine fishes. Fish are grouped by Order, Family, then by Species, and are identified as either being reared (R) or from collections of wild (W) fish. For each species the levels of data resolution (species, population and individual levels) available in the literature are listed. Intraspecific comparisons are divided into among population (AP) and within population (WP) comparisons, and the number of observations included at each level for a given species are listed. Information on the average temperature during larval growth is presented for the species for which it was available, along with the references for each species.

			Interspecific			Intraspecific			
Order					SD	SD		T(°C)	
Family	Species	R/W	AM	LM	$_{AM}$	$_{LM}$	AP	WP	Source [1]
Acanthuroidei									
Acanthuridae	Naso sp.[a]	W	Y	Y					6
Balistoidei									

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
Monacanthidae	Monacanthus chinensis[a]	W	Y	Y						6
	Paraluteres prionurus[a]	W	Y	Y						6
	Parika scaber[a]	W	Y	Y	Y	Y	2	3		15[b c]
Beryciformes										
Holocentridae	Holocentrus ascensionis[a]	W	Y		Y					32[b]
	Holocentrus rufus[a]	W	Y		Y					32[b]
Blennioidei										
Blenniidae	Petroscirtes mitratus[a]	W	Y	Y		Y				6
Gobiidae	Amblygobius rainfordi[a]	W	Y	Y	Y	Y				6
	Awaous stamineus[a]	W	Y		Y					25
	Coryphopterus glaucofraenum[a]	W	Y	Y	Y					27

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	Gobidon sp. A[a]	W	Y	Y						6
	Gobidon sp. B[a]	W	Y	Y						6
	Gobidon sp. C[a]	W	Y	Y						6
	Paragobidon echinocephalus	W	Y	Y						6
	P. lacunicola	W	Y	Y						6
	P. melanosoma	W	Y	Y	Y	Y				6
	Sicydium antillarum	W	Y	Y	Y	Y	4	4		3
	S. punctatum	W	Y	Y	Y	Y	10	10		3
	Stenogobius genivittatus[a]	W	Y		Y					25
	Unidentified[a]	W	Y	Y	Y	Y				6

Appendix 1. continued

Family	Species	R/W	AM LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
Labroidei									
Labridae	Anampses cuvier[a]	W	Y	Y					35
	A. twistii[a]	W	Y	Y					35
	Bodianus axillaris[a]	W	Y	Y					35
	B. bilunulatus[a]	W	Y	Y					35
	B. diplotaenia[a]	W	Y	Y					35
	B. mesothorax[a]	W	Y	Y					35
	B. rufus[a]	W	Y	Y					35
	Cheilinus bimaculatus[a]	W	Y	Y		2			35
	C. chlorourus[a]	W	Y	Y					35
	C. diagrammus[a]	W	Y	Y					35
	C. fasciatus[a]	W	Y	Y					35

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	C. trilobatus[a]	W	Y		Y					35
	C. undalatus[a]	W	Y		Y					35
	C. unifasciatus[a]	W	Y		Y					35
	Cheilio inermis[a]	W	Y		Y					35
	Choerodon anchorago[a]	W	Y		Y					35
	Cirrhilabrus cyanopleura[a]	W	Y		Y					35
	C. temminki[a]	W	Y	Y	Y	Y				6
	Clepticus parrae[a]	W	Y		Y					35
	Coris flavovittata[a]	W	Y		Y					35
	C. gaimard[a]	W	Y		Y		2			35
	C. variegata[a]	W	Y	Y	Y	Y	2			6, 35

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	C. venusta[a]	W	Y	Y						35
	Cymolutes lecluse[a]	W	Y	Y						35
	C. praetextatus[a]	W	Y	Y						35
	Diproctacanthus xanthurus[a]	W	Y	Y						35
	Doratonotus megalepis[a]	W	Y	Y						35
	Epibulus insidiator[a]	W	Y	Y						35
	Gomphus varius[a]	W	Y	Y			2			35
	Halichoeres argus[a]	W	Y	Y						35
	H. biocellatus[a]	W	Y	Y						35
	H. bivittatus[a]	W	Y	Y						35
	H. chierchiae[a]	W	Y	Y						35

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	H. chloropterus[a]	W	Y		Y					35
	H. chrysus[a]	W	Y		Y					35
	H. dispilus[a]	W	Y		Y					35
	H. garnoti[a]	W	Y		Y					35
	H. hoeveni[a]	W	Y	Y	Y	Y				6
	H. hortulanus[a]	W	Y		Y					35
	H. maculipinna[a]	W	Y		Y					35
	H. margaritaceus[a]	W	Y		Y					35
	H. marginatus[a]	W	Y		Y					35
	H. melanurus[a]	W	Y		Y					35
	H. nebulosus[a]	W	Y		Y					35

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	H. nicholsi[a]	W	Y		Y					35
	H. ornatissimus[a]	W	Y		Y					35
	H. pictus[a]	W	Y		Y					35
	H. poeyi[a]	W	Y		Y					35
	H. prosopeion[a]	W	Y		Y					35
	H. radiatus[a]	W	Y		Y					35
	H. richmondi[a]	W	Y		Y					35
	H. scapularis[a]	W	Y		Y					35
	H. semicinctus[a]	W	Y		Y					35
	H. trimaculatus[a]	W	Y		Y					35
	Hemigymnus fasciatus[a]	W	Y		Y					35

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	Hemigymnus melapterus[a]	W	Y		Y					35
	Labrichthys unilineatus[a]	W	Y		Y					35
	Labroides bicolor[a]	W	Y		Y					35
	L. dimidiatus	W	Y	Y	Y	Y	2			6, 35
	L. pectoralis[a]	W	Y		Y					35
	L. phthirophagus[a]	W	Y		Y					35
	Labropsis micronesica[a]	W	Y							35
	L. xanthonota[a]	W	Y		Y					35
	Lachnolaimus maximus[a]	W	Y		Y					35
	Macropharyngodon geoffroy[a]	W	Y		Y					35
	M. meleagris[a]	W	Y		Y					35

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	M. negrosensis[a]	W	Y							35
	Novaculichthys macrolepidotus[a]	W	Y		Y					35
	N. taeniourus[a]	W	Y		Y		2			35
	Oxyjulis californic[a]	W	Y		Y					35
	Pseudocheilinus evanidus[a]	W	Y		Y		2			35
	P. hexataenia[a]	W	Y		Y					35
	P. octotaenia[a]	W	Y		Y		2			35
	P. tetrataenia[a]	W	Y		Y					35
	Pseudojulis melanotis[a]	W	Y		Y					35
	P. notospilus[a]	W	Y		Y					35
	Pseudojuloides cerasinus[a]	W	Y		Y					35

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	Pteragogus cryptus[a]	W	Y		Y					35
	P. flagellifera[a]	W	Y		Y					35
	P. guttatus[a]	W	Y		Y					35
	Semicossyphus pulcher[a]	W	Y	Y	Y	Y	2	1		8, 35
	Stethojulis balteata[a]	W	Y		Y					35
	S. bandanensis[a]	W	Y		Y					35
	Stethojulis sp.[a]	W	Y	Y						6
	S. strigiventer[a]	W	Y		Y					35
	Tautoga onitis	W	Y		Y					35
	Tautogolabrus adspersus	W	Y		Y					35
	Thalassoma amblycephalum[a]	W	Y		Y					35

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	T. ballieui[a]	W	Y		Y					35
	T. bifasciatum[a]	W	Y	Y	Y	Y	3	1		33, 34
	T. duperrey[a]	W	Y		Y					35
	T. hardwicke[a]	W	Y		Y					35
	T. janseni[a]	W	Y		Y					35
	T. lucasanum[a]	W	Y		Y		4			35, 37
	T. lunare[a]	W	Y	Y	Y	Y	2			6, 35
	T. lutescens hybrid?[a]	W	Y							35
	T. quinquevittatum[a]	W	Y		Y					35
	T. trilobatum[a]	W	Y		Y					35
	Unidentified[a]	W	Y	Y	Y	Y				6

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	Xyrichtys martinicensis[a]	W	Y		Y					35
	X. novacula[a]	W	Y		Y					35
	X. pavoninus[a]	W	Y		Y		2			35
	X. splendens[a]	W	Y		Y					35
Pomacentridae	Abudefduf abdominalis	W	Y		Y		2			30, 36
	A. saxatilis	W	Y	Y	Y	Y	3	1		6, 30, 36
	A. sexfasciatus[a]	W	Y		Y					36
	A. sordidus[a]	W	Y		Y					36
	A. taurus	W	Y	Y	Y	Y	2			30, 36
	A. troschelii[a]	W	Y		Y					36
	A. vaigiensis[a]	W	Y	Y	Y		2			30, 36
	Amblyglyphidodon curacao	W	Y	Y	Y	Y	2	1		30, 36

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	A. leucogaster[a]	W	Y		Y					30, 36
	A. ternatensis[a]	W	Y	Y	Y					36
	Amphipiron chrysopterus	W		Y						30
	A. percula	W	Y	Y						30
	A. perideraion	W	Y	Y						30
	A. polymnus[a]	W	Y	Y						30
	A. tricinctus	W	Y	Y						30
	A. clarkii[a]	W	Y	Y	Y	Y				36
	A. melanopus[a]	W	Y	Y	Y	Y				36
	A. perideraion[a]	W	Y		Y					36
	Cheiloprion labiatus[a]	W	Y	Y	Y					36
	Chromis agilis[a]	W	Y		Y					36

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	C. alta[a]	W	Y		Y					36
	C. atrilobata[a]	W	Y		Y					36
	C. atripectoralis[a]	W	Y	Y	Y	Y	3			29, 30
	C. atripes[a]	W	Y	Y	Y	Y				36
	C. caudalis[a]	W	Y		Y					36
	C. cyanea[a]	W	Y	Y	Y	Y				36
	C. delta[a]	W	Y		Y					36
	C. insolata[a]	W	Y		Y					36
	C. lepidolepis[a]	W	Y	Y	Y	Y				36
	C. limbaughi[a]	W	Y		Y					36
	C. lineata[a]	W	Y		Y					36

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	C. margaritifer[a]	W	Y	Y	Y	Y				36
	C. multilineata[a]	W	Y	Y	Y					36
	C. punctipinnis	W	Y		Y					36
	C. retrofasciata[a]	W	Y		Y					36
	C. sp,[a]	W	Y	Y	Y	Y				6
	C. ternatensis[a]	W	Y	Y	Y		2			30, 36
	C. vanderbilti[a]	W	Y		Y					36
	C. viridis	W	Y	Y	Y		2			30, 36
	C. weberi[a]	W	Y		Y					36
	C. xanthura[a]	W	Y		Y					36
	Chrysiptera biocellatus	W	Y		Y		2			30, 36
	C. cyanea	W	Y	Y	Y	Y	2			30, 36

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	C. glauca[a]	W	Y		Y					36
	C. leucopoma	W	Y		Y		2			30, 36
	C. oxycephala[a]	W	Y	Y	Y	Y				36
	C. rex[a]	W	Y	Y	Y	Y				36
	C. rollandi	W	Y	Y						30
	C. talboti[a]	W	Y	Y						30
	Dascyllus albisella[a]	W	Y		Y		2			30, 36
	D. arunanus[a]	W	Y	Y	Y	Y	3	1		6, 30, 36
	D. melanurus	W	Y	Y	Y	Y	2			30, 36
	D. reticulatus[a]	W	Y	Y	Y	Y		1		36
	D. trimaculatus[a]	W	Y	Y	Y	Y	2			30, 36
	Dischistodus chrysopoecilus[a]	W	Y	Y	Y	Y		1		36

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	D. melanotus[a]	W	Y	Y	Y					36
	D. perspicillatus[a]	W	Y	Y	Y	Y				36
	D. pseudochrysopoecilus	W	Y	Y	Y	Y	3			6, 30, 36
	Glyphidodontops rollandi[a]	W	Y	Y	Y	Y				6
	G. talboti[a]	W	Y	Y						6
	Hemiglyphidodon plagiometopon[a]	W	Y	Y	Y	Y				36
	Hypsypops rubicundus[a]	W	Y		Y					36
	Microspathodon chrysurus	W	Y	Y	Y		2			30, 36
	Neopomacentrus azysron[a]	W	Y	Y			2			6, 30
	N. nemurus[a]	W	Y	Y	Y	Y		1		30, 36
	Paraglyphidodon melas	W	Y	Y	Y	Y				30, 36
	P. nigrosis[a]	W	Y	Y	Y	Y				36

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	Plectoglyphidodon dickii[a]	W	Y		Y					36
	P. imparipennis	W	Y		Y					36
	P. lacrymatus[a]	W	Y		Y					36
	Pomacentrus alexanderae[a]	W	Y	Y	Y	Y		1		36
	P. amboinensis	W	Y	Y	Y	Y	4			6, 30, 36
	P. arenarius	W	Y	Y						30
	P. australis[a]	W	Y	Y	Y		2			6, 30
	P. bankanensis[a]	W	Y	Y	Y	Y				36
	P. burroughi[a]	W	Y		Y					36
	P. coelestis[a]	W	Y	Y	Y	Y	4			29, 30, 36
	P. emarginatus[a]	W	Y	Y	Y	Y				36
	P. grammorhynchus[a]	W	Y		Y					36

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	P. moluccensis[a]	W	Y	Y	Y	Y	2	1		30, 36
	P. pavo[a]	W	Y	Y	Y	Y	2	1		30, 36
	P. popei[a]	W	Y	Y	Y	Y				6
	P. rhodonotus	W	Y	Y	Y	Y	2			30, 36
	P. simsiang[a]	W	Y	Y	Y	Y				36
	Pomacentrus sp. 1[a]	W	Y	Y	Y	Y				36
	Pomacentrus sp.[a]	W	Y	Y	Y	Y				6
	Pomacentrus sp.[a]	W	Y	Y	Y	Y				6
	P. taeniometopon[a]	W	Y		Y					36
	P. vaiuli[a]	W	Y	Y	Y	Y	2			30, 36
	P. wardi	W	Y	Y	Y	Y	2			6, 30

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	Stegastes acapulcoensis[a]	W	Y		Y					36
	S. arcifrons[a]	W	Y		Y					36
	S. diencaeus	W	Y	Y	Y	Y	2			30, 36
	S. dorsopunicans[a]	W	Y	Y	Y	Y				36
	S. fasciolatus[a]	W	Y		Y					36
	S. flavilatus[a]	W	Y		Y					36
	S. leucorus beebei[a]	W	Y		Y					36
	S. leucostictus[a]	W	Y	Y	Y	Y	2	1		30, 36
	S. partitus	W	Y	Y	Y	Y	3			30
	S. planifrons	W	Y	Y	Y	Y	2			30, 36
	S. redemptus[a]	W	Y		Y					36
	Stegastes sp.[a]	W	Y		Y					36

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	S. variabilis[a]	W	Y	Y	Y	Y	2			30, 36
Scaridae	Unidentified[a]	W	Y	Y	Y	Y				6
	Unidentified[a]	W	Y	Y	Y	Y				6
Percoidei										
Apogonidae	Apogon cyanosoma[a]	W	Y	Y	Y	Y				6
	A. doerderlieni[a]	W	Y	Y	Y	Y				6
	Cheilodipterus quinquelineata[a]	W	Y	Y	Y	Y				6
	Unidentified[a]	W	Y	Y		Y				6
Chaetodontidae	Chaetodon plebiusa	W	Y	Y	Y		2			6, 11
	C. rainfordi[a]	W	Y	Y	Y		2			6, 11
	Chelmon rostratus[a]	W	Y	Y	Y	Y	2			6, 11
Haemulidae	Haemulon flavolineatum	W	Y	Y						5

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
Lethrinidae	Lethrinus nebulosus	W	Y	Y						6
Lutjanidae	Unidentified[a]	W	Y	Y		Y				6
Mullidae	Upeneus tragula	W/R	Y	Y	Y	Y	10	1	25, 30	18, 19[b]
Nemipteridae	Scolopsis dubiosus[a]	W	Y	Y	Y	Y				6
Sparidae	Pagrus major	W	Y	Y		Y			20.5	12-2
Pleuronectiformes										
Paralichthys	Paralichthys dentatus	R	Y	Y	Y	Y	5		6.6-16.6	14
	Paralichthys olivaceus	R	Y	Y			3		12.6-19.1	26
Pleuronectidae	Ammotretis rostratus	R	Y	Y			2		14.6, 16.7	9
	Eopsetta jordani	W	Y	Y		Y				23[d]
	Glyptocephalus zachirus[a]	W	Y	Y		Y				23[d]
	Limanda herzensteini[a]	R	Y	Y						20

Appendix 1. continued

Family	Species	R/W	AM	LM	SD AM	SD LM	AP	WP	T(°C)	Source [1]
	L. yokohamae	R	Y	Y	Y	Y			12.1	12-1[b]
	Microstomus pacificus[a]	W	Y	Y		Y				23[d]
	Platichthys stellatus	R	Y	Y	Y	Y	9	9	9.5-12.0	24
	Pleuronectes americanus	R	Y	Y	Y	Y	21	19	5-8.8	4, 7, 17
	P. platessa	R	Y	Y		Y	3			13[c], 20
	Rhombosolea tapirina	R	Y	Y			2		12.5, 15.2	9
Scophthalmidae	Scophthalmus maximus	R	Y	Y						16
Soleidae	Heteromycteris japonicus[a]	R	Y	Y						20
	Solea solea	W/R	Y	Y	Y	Y	21		7-22	1, 2, 10

[a] hatching length was estimated from the family mean length at hatching

[b] summary statistics (mean, SD) were extracted from a Figure or a Table

[c] metamorphic age was calculated from an age-length regression provided in the text

Appendix 1. continued

[d] estimates of age at metamorphosis are poor

[1]Sources:1-Amara and Lagardère (1995); 2-Amara et al. (1993); 3-Bell et al. (1995); 4-Bertram et al. (1993); 5-Brothers and McFarland (1981); 6-Brothers et al. (1983); 7-Chambers and Leggett (1987); 8-Cowen (1991); 9-Crawford (1984); 10-Fonds (1979); 11-Fowler (1989); 12-1 Fukuhara (1988); 12-2 Fukuhara (1991); 13-Hovenkamp (1990); 14-Keefe and Able (1993); 15-Kingsford and Milicich (1987); 16-Kuhlman et al. (1981); 17-Laurence (1975); 18-McCormick (1994); 19-McCormick and Molony (1995); 20-Minami and Tanaka (1992); 21-Minami et al. (1988); 22-Noichi et al. (1997); 23-Pearcy et al. (1977); 24-Policansky (1982); 25-Radtke et al. (1988); 26-Seikai et al. (1986); 27-Sponaugle and Cowen (1994); 28-Tanaka et al. (1989); 29-Thorrold and Milicich (1990); 30-Thresher and Brothers (1989); 31-Thresher et al. (1989); 32-Tyler et al. (1993); 33-Victor (1982); 34-Victor (1986a); 35-Victor (1986b); 36-Wellington and Victor (1989); 37-Wellington and Victor (1992)